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LIMITING FACTORS IN RELATION TO SPECIFIC RANGES OF TOLERANCE OF FOREST TREES

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(WITH SEVEN FIGURES)

The conclusions recorded in this paper are drawn from a study of the forests throughout the Province of Ontario, particularly along the shores of Lake Ontario, Lake Simcoe, the Kawartha Lakes, and Rideau Lakes; in Algonquin Park and in Mattagami and Timagami Forest Reserves. Observations, with notes, have been made during more than 6000 miles of travel by canoe and overland through the forest country of northern Ontario, especially along the streams and lakes forming the headwaters of the Muskoka, Maganatawan, Petewawa, and Madawaska rivers; also of the Montreal, Sturgeon, Wanapitei, Vermilion, Mattagami, and Abitibi rivers. While the greater part of the discussion has particular reference to Ontario, the conclusions are made in the light of some personal knowledge of the forests southward to the Gulf of Mexico and westward to the Pacific.

The data regarding the limits of forest trees recorded in the accompanying maps have been obtained principally from accounts of the explorations of BELL (2), MACOUN (19, 20), and LOW (18). The records of isotherms and precipitation areas have been copied from the Geological Atlas of Canada, 1915. So far as the writer

has been able to observe, the records of the explorers mentioned have been even more accurate than has generally been conceded. Although the specific limits of forest species have been rather definitely outlined, there seems to be no agreement regarding the part played in determining these limits by the various factors affecting forest growth. In this paper an attempt has been made to relate the limiting factors to the specific range of tolerance of forest trees, and in this way to account for the respective distributions of some of the species dominating the forests of Ontario.

SCHIMPER (21), as a result of his extensive studies in plant geography, concludes that "the differentiation of the earth's vegetation is thus controlled by 3 factors: heat, atmospheric precipitation (including winds), soil. Heat determines the flora, climatic humidity the vegetation; the soil as a rule merely picks out and blends the materials supplied by these two climatic factors, and on its own account adds a few details."

Investigators have mentioned many factors which affect the composition of forests. Drawing his conclusions from the exploration of Labrador, LOW (18) says "the distribution of forest areas and the range of the various trees depend upon several factors, among which may be mentioned position as regards latitude, height above the sea coast, and the character of the soil." BOWMAN (3) in the light of his physiographic studies says as follows:

> The distribution of forests is controlled largely by rainfall, although the distribution of species within each region is also controlled by insolation, temperature, wind velocity, water supply, and geographic relation to postglacial centers of distribution. When more detailed statements are attempted many difficulties are encountered in the form of apparent inconsistencies. Some species appear to find their appropriate conditions in different latitudes by a change in their habitat; for example, the larch, balsam fir, and white birch which in the north grow freely on dry or hilly ground, toward the southern limits seek the cold ground in swamps. The white cedar and white pine in some places manifest the same tendency.

FROTHINGHAM (12) in his report on hardwood forests sums up the situation as follows: "How moisture and temperature affect the different species in the complexity of forest environment is still so little known that no positive information can be given."

Temperature factor

The northern limits of many tree species are undoubtedly the result of low temperatures. WARMING (24) states, "It is clear that conditions as regards heat determine the boundaries of the distribution of species on the earth." The effect of temperature is emphasized by the fact that "the appropriate temperature for the growth of a number of species, such as *Picea* and *Abies*, is carried far to the south of their normal latitudes along the elevated parts of the continent, especially the Alleghanies and Rocky Mountains" (BELL 2). In such regions the tree species are in most cases identical with those found farther north. However, it is more difficult to account for the southern limits of trees on a basis of minimum temperature. BRAY (5) finds difficulty in explaining the occurrence of boreal (*Picea*, *Abies*) assóciations in the bogs of regions dominantly austral. "The question arises as to whether the factor of temperature plays a rôle in the occurrence of these bogs," and again, "the extremely irregular boundary between the boreal conifer forests and the temperate hardwood forests of New England, for example, can hardly be explained by temperature alone" (HARPER 14).

The lines representing the limits of *Picea nigra*, *Larix americana*, and *Betula papyrifera* follow yearly isotherms very closely from the mouth of the Mackenzie River across the continent until they reach the coast of Labrador, where they swing southward, here following a course almost parallel with the coast line. There is reason to believe that temperature is the limiting factor throughout a great area, while a second factor is active along the Labrador coast. From the fact that the same order in the limitation of these species is retained, even in the Labrador region, it would seem that the limiting factors are similar throughout. Excessive loss of heat energy due to the air currents so prevalent in this region has the same effect as the loss of heat energy due to excessively low temperatures. Similarly in southern Ontario, where latitude and lake influence together result in a region of a relatively high yearly temperature average, the limits of trees such as *Juglans nigra* and *Castanea dentata* are parallel with isotherms. Here also the evidence would indicate that temperature is the limiting factor with

respect to such species. The general conclusion that temperature is usually, if not universally, the determinant of northern limits has resulted from making general statements based upon selected and favorable instances which are specific rather than general.

There is abundant evidence that while temperature acts as a limiting factor in many instances, it is by no means the only factor controlling even the northern limits of tree species. This is amply demonstrated by the data recorded on the accompanying map (fig. 1). Many of the lines indicating the northern limits of tree species intersect; this cannot be accounted for on a temperature basis. Isotherms do not intersect nor do lines indicating the length of the growing season. The northern limit of *Pinus Banksiana* at 100° W. long. traverses a region the yearly isotherm of which is 25° F.; at 80° W. long. the isotherm which the northern limit traverses is 32.5° F.; at 75° W. long. it is 20° F.; and at 70° W. long. it reaches the 32.5° F. isotherm. The isotherms corresponding to the northern limits of *Ulmus americana* at various regions are at 100° W. long. 27.5° F.; at 95° W. long. 32.5° F.; at 80° W. long. 30° F.; at 75° W. long. 40° F.; and at 70° W. long. 32.5° F., a remarkable range of variation. The looping of the lines representing the limits of such species as *Picea canadensis*, *Populus balsamifera*, and *Populus tremuloides*, as shown in the Labrador region (northern Quebec), is significant, particularly in the case of *Picea canadensis*, in contrast with the closely related *Picea mariana*. The northward deviation of the limits for *Betula lutea*, *Acer saccharum*, *Tsuga canadensis*, and *Quercus rubra* at 80° W. long., a point where the isotherm swings southward, cannot be explained on a temperature basis. The anomalous tree distribution in the Saugenay region is another case in point. Any idea of the possibility of explaining the western limits on a temperature basis has long been discarded. It is evident that in the instances mentioned something other than temperature must be the limiting factor.

Water factor

Water as a factor in the determination of tree distribution has received considerable recognition. COWLES (**8**) says, "On the whole there has been a general tendency to overestimate the influence of

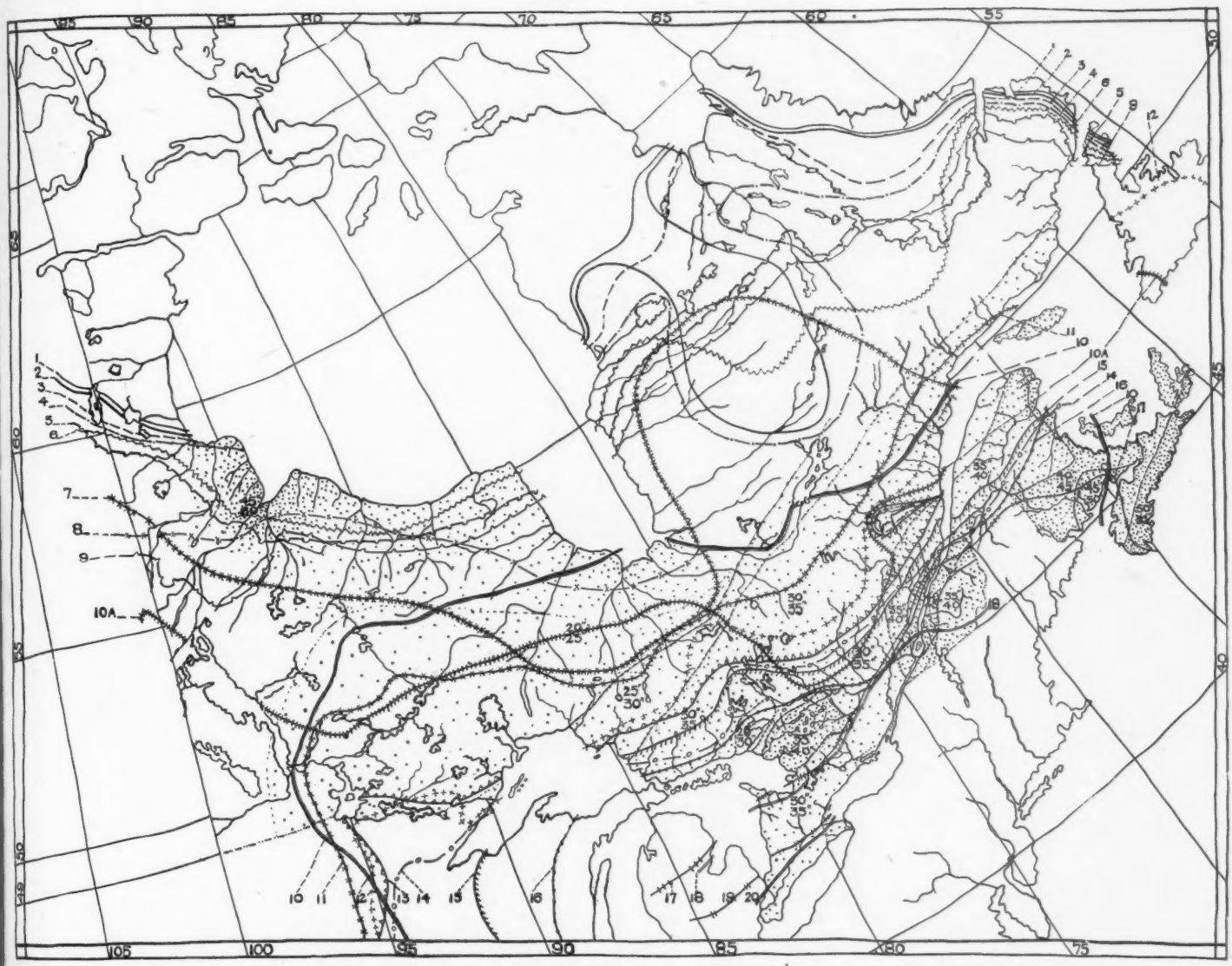

FIG. 1.—Northern limits of tree species represented by lines having identification numbers and marks: *o*, original; *r*, revised; isobars outlined by connected dots and average yearly temperature indicated in degrees; 1, *Picea mariana;* 2, *P. canadensis;* 3, *Larix americana;* 4, *Populus balsamifera;* 5, *Betula papyrifera;* 6, *Populus tremuloides;* 7, *Pinus Banksiana;* 8, *P. Banksiana* (other data and outliers); 9, *Abies canadensis;* 10, *Thuja occidentalis;* 10A, *Ulmus americana;* 11, *Pinus Strobus;* 12, *Betula lutea;* 13, *Acer saccharum;* 14, *Quercus rubra;* 15, *Tsuga canadensis;* 16, *Fagus americana;* 17, *Juglans cinerea:* 18, *Carya amara;* 19, *Juglans nigra;* 20, *Castanea dentata*

temperature as an ecological factor. The trend of nearly all experiment has been to show that water is of vastly greater importance." BELL (2) states, "A great difference in the moisture of the air of two regions otherwise resembling each other in climatic conditions has also a powerful effect upon the growth of forests; and the dryness of the air in the western prairie and arid regions is, no doubt, the chief cause of the absence of timber."

There has been much recent research concerned with the water relation of plants (9). The greater number of investigators have selected the region of the great plains, a region where water is dominantly the limiting factor, as their field of investigation. TRANSEAU (22, 23), LIVINGSTON (16, 17), and FULLER (13) have shown that the water factor may be regarded as a complex depending primarily upon the amount of soil water available for the plant and the rate of evaporation. The amount of available soil water is dependent upon precipitation during the growing season and the physical properties of the soil, while evaporation depends chiefly upon the humidity, air currents, and temperature of the atmosphere. BRIGGS and SHANTZ (4) in their work on the wilting coefficient have emphasized the specificity of tolerance in plants with respect to minimum soil water. The valuable experimental data recorded in these papers demonstrate that water frequently acts as a limiting factor; the converse, that there is a considerable range for any given species wherein water does not factor in a limiting capacity, is less frequently emphasized.

It is significant that the limits of tree species such as *Picea mariana*, *P. canadensis*, *Larix americana*, *Populus balsamifera*, *Abies canadensis*, and *Betula papyrifera*, which extend north of the arid plains, are not deflected southward in the Manitoba-Minnesota region, while almost invariably the more southern species are deflected when they come in contact with the region of diminished precipitation. The evidence would indicate that the water factor limits the westward extension of such species as *Acer saccharum*, *Tsuga canadensis*, *Fagus americana*, *Thuja occidentalis*, and *Ulmus americana*.

It may be noted, also, that when this deflection takes place the order in which the tree limits occur is changed in many instances.

Thuja occidentalis, which extends northward far beyond *Acer saccharum*, does not reach the western limits of the latter, while *Quercus rubra* extends westward beyond the limits of many species which are to be found beyond its northern limit. Such phenomena doubtless are the result of the fact that different limiting factors dominate the several regions forming the boundaries of distribution.

In southeastern Canada it is difficult to find any parallelism between the limits of tree species and the boundaries of precipitation areas. For instance, *Juglans cinerea* extends throughout areas whose respective yearly precipitations are 30–35 in., 35–40 in., 30–35 in., 40–45 in., and 45–50 in., with no apparent deflection of the lines bounding its growth area. The limits of *Fagus americana* pass through similar areas, with the addition of an area where the minimum yearly precipitation is 25 in. This range is of particular significance in consideration of the fact that *Fagus* is generally regarded as mesophytic. The absence of a parallelism between precipitation and forest limits in the Ontario section is so obvious from a consideration of the accompanying map (fig. 2) that further emphasis would be superfluous. Other conditions being favorable, there is sufficient rainfall for forest growth; or, in other words, precipitation does not enter here as a limiting factor.

WARMING (24) has based his ecological classification of plants upon the premise that "the most potent and decisive factor is the amount of water in the soil." "The soil upon which the coniferous forest occurs varies widely, yet so far as reliable information is available it is always physically or physiologically dry." "The cold winter is a physiologically dry season against which trees can protect themselves by defoliation or by xerophytic structure." This may account for the xerophytic structure of the coniferous leaf; it is difficult to understand what bearing it has in connection with the contention that conifers as a class grow in dry soil conditions, the winter, even for conifers, being a period of comparative dormancy. Deciduous trees are protected against the "physiological dryness" of winter by leaf fall; conifers by having leaves of xerophytic structure. Some deciduous trees, for example *Quercus*, are comparatively xerophytic, while others are decidedly meso-

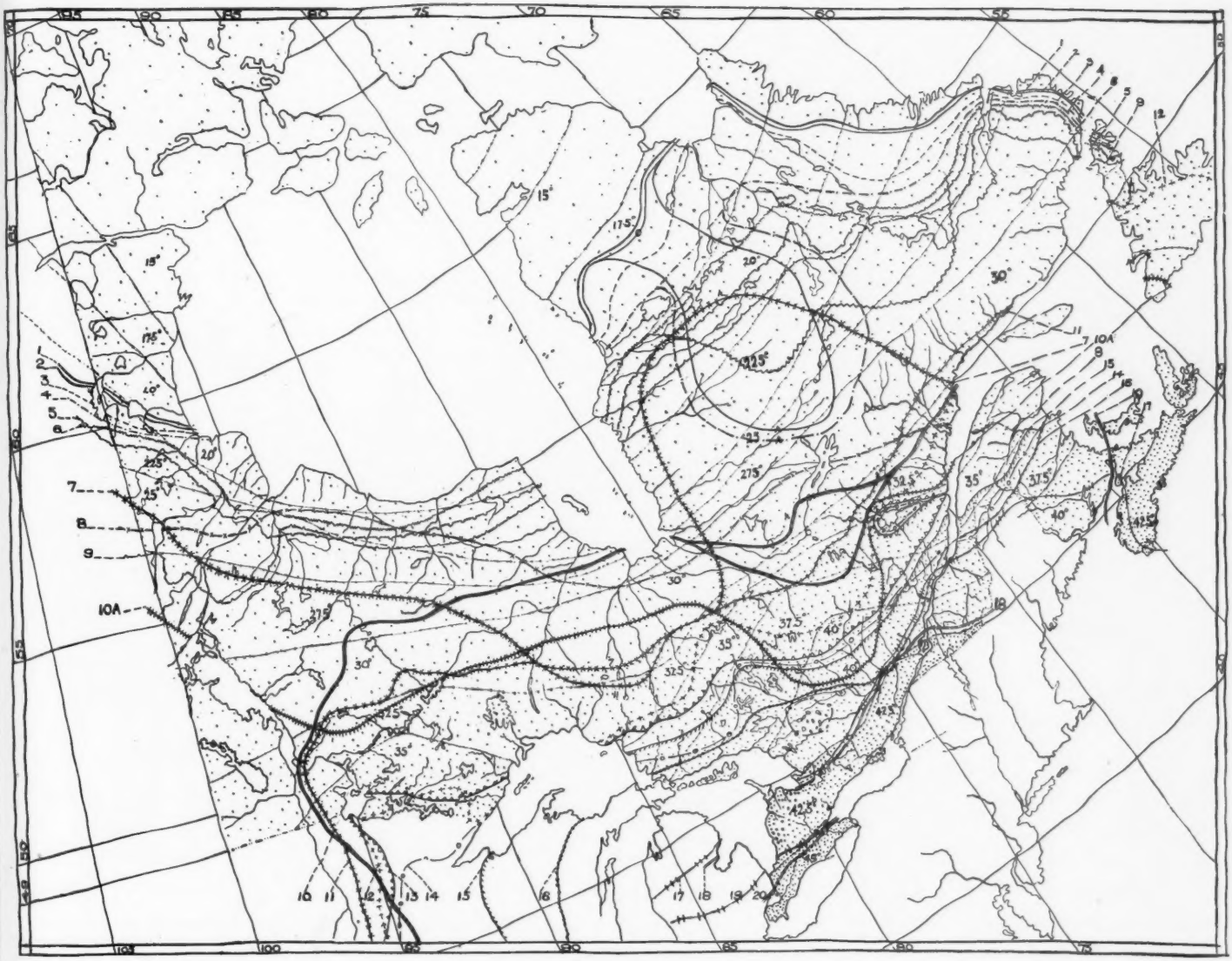

FIG. 2.—Similar to fig. 1 except that a precipitation rather than a temperature map is superimposed upon the chart of tree limits; numbers indicate precipitation in inches.

phytic, as *Fagus* and *Acer*. It seems possible that there might be a similar range amongst conifers. ZON (27) states, "Balsam fir attains its best growth and largest size on flats the soil of which is usually a moist, deep sand-loam." An abundance of available soil water is not the factor which so often excludes *Abies balsamea* from such soils, particularly in the more temperate regions.

During the summer of 1914 a series of experiments were conducted in Algonquin Park to discover the relation of seedling growth to atmospheric humidity. Atmometers of the LIVINGSTON design were set up at a number of stations, including those where seedlings of *Acer saccharum*, *Abies balsamea*, and *Picea mariana* were abundant. The readings for the months of July, August, and part of September proved that in this region there is no appreciable difference in the rates of evaporation at the stations mentioned, and that in each case the humidity was in excess of that which FULLER (13) regards as characteristic of a mesophytic forest. Moreover, *Acer* grows on the more exposed ridges; *Abies* and *Picea* on the less exposed lowlands or slopes. Experiment has shown that such conditions hold generally for the "lake country," where in many cases one-tenth of the total area is covered by water, and the greatest distance of any point from bodies of water seldom exceeds 2 miles. Three of the limiting factors most frequently emphasized, temperature, atmospheric humidity, and precipitation, are eliminated, as such, under conditions prevailing, and still there is a marked segregation of forest associations.

Soil factor

The problem regarding the extent to which soil composition may act as a limiting factor in the determination of forest distribution has been variously answered. FROTHINGHAM (12) states "The soils of the northern hardwood forest are as a rule loamy sands, the results of the decay of granite, quartzites, and siliceous gneisses, also the water assorted loams and clays or the unassorted morainal tills, rich in clay; but they also thrive on light sandy soil in localities subject to moist winds." In connection with the forests of Michigan, BEAL and WHEELER (1) state that "The best wheat lands are usually found on uplands near

streams, where the oak timber gradually shades into beech and maples." On the other hand, "evergreen trees, whether coniferous or broad-leaved, seem to be just as characteristic of poor soil as of any particular kind of climate" (14). BOWMAN (3) draws attention to the limitations of soil composition as a determining factor. COWLES has shown that the composition of the rock from which any soil may be derived seldom acts in a limiting capacity with respect to the species which that soil may support. It is only in exceptional cases that a soil, newly weathered, is deficient in the mineral constituents necessary for plant growth. This generalization is particularly applicable in Ontario, where the soil, whether it be glacial drift toward the south, or the weathered deposits and exposed rocks farther north, is derived from the dominantly granitic rock of the Laurentian Plateau. The original composition of the soil is seldom a limiting factor, at least in so far as the forests of Ontario are concerned.

Humus factor

It is scarcely necessary to emphasize the importance of the humus content of the soil as an ecological factor; its significance as a limiting factor with respect to the forests of Ontario is our chief concern. In forest regions the humus content of the soil increases the water retaining capacity; increases the porosity, and hence the aeration of the soil. Mineral salts are retained by the adsorptive properties of humus, and incidentally, conditions are made more favorable for soil bacteria, which are essential for the growth of such species as *Fagus*. COWLES (8) states, "Although bare sand supports a xerophytic flora, the accumulation of a thin humus layer is sufficient for forest development, and the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune if there is present a humus layer a few centimeters in thickness." In the Algonquin Park region to which reference has been made, the *Acer* or *Acer-Fagus* forest occupies the ridges, while the *Abies-Picea* forest occupies the lower slopes and lowlands. On the slopes where the exposure of the rocks, due to drainage of glacial lakes, has been comparatively recent, only a small amount of rock soil has accumulated; this is covered by a humus layer, but the two are not intimately intermingled by weathering processes. The

humus content of the soil proper is low. In the lowlands a similar condition maintains. This is especially applicable to the peat bog, where humus is most abundant. There has been no movement, however, of the particles of the contiguous strata of the rock soil and the overlying humus; they are distinct, hence the otherwise valuable humus is practically useless in so far as the improvement of soil properties is concerned. On the ridges which were exposed first by the subsidence of glacial ice and water there is much deeper soil, and the humus accumulated from antecedent vegetation has become intimately associated with the rock soil by weathering. The soil proper has a high humus content and is able to support such trees as *Acer* and *Fagus*. It will be remembered that the temperature, precipitation, humidity, and original soil composition may be regarded as constant; the varying factors are those associated with the accumulation of humus. The humus content of the soil is at least a local factor in the determination of tree distribution.

It has been maintained that differences in the composition of soil have only a local effect. It does not seem clear why a factor which is potent locally should not be potent throughout greater areas. The gradients of soil changes are usually greater when limited areas are considered; hence also those of the associated floral changes. The Laurentian Plateau is a great area dominated by the coniferous forest, while the contiguous region of glacial drift is dominated by the deciduous hardwood forest. The marked differences in forest species prevailing in the regions north and south of the Kawartha Lakes, respectively, is strikingly in accord with soil differences. Moreover, the line separating the dominantly coniferous region from the dominantly deciduous hardwood region does not follow any isotherm or the boundaries of any precipitation area, but rather the outlines of the Laurentian Plateau, roughly from the southeast part of Georgian Bay to Lake Simcoe along the Kawartha Lakes, southeastward to the Thousand Islands, northward to Ottawa, and again eastward along the northern limits of the Ottawa and St. Lawrence valleys. In the coniferous region there are oases of deciduous hardwoods of considerable area, such as that at Renfrew, or of limited area, such as the ridges already mentioned; in fact, wherever the soil is similar to that found in the

characteristically deciduous hardwood area. It is true that these broad outlines have been obscured in many places by large tracts being covered with pioneer forms, such as *Populus* and *Betula*, as a result of "burns" (10, 11, 15). These regional forest limitations cannot be explained except upon some basis of soil differences, such as have been described as determining the local limitations of the forest types of Algonquin Park. The evidence clearly indicates that the slowly weathering rock of the Laurentian Plateau has been a barrier against migration of the hardwood forest, which, however, has been able to establish outposts where favorable soil conditions have been found. In brief, the development of a soil, particularly with reference to its humus content, may act as a limiting factor regionally as well as locally.

Light factor

It is generally accepted that seedlings of some tree species grow only where there is abundance of light, while others grow best under shade conditions (26). FROTHINGHAM (12) has classified the trees of the northern hardwood forest upon the basis of light tolerance. The seedlings of pioneer species are necessarily light tolerant in contrast with those species forming the climax forest, which are shade tolerant; seedlings of *Pinus Banksiana* and *P. Strobus* thrive only in direct sunlight, which is also the case with seedlings of *Abies balsamea* and *Picea canadensis*, although to a less marked degree. On the other hand, the seedlings of *Acer* and *Fagus* grow best in the dense shade of mature trees; *Tsuga canadensis* is an example of a conifer which is similar in this respect. Because of the specificity of the range of tree species with respect to intensity of light, certain forms cannot be pioneers, while others are eliminated from forests which have been well established, except where destructive agencies such as cause windfalls and erosion are at work. To this extent the intensity of light may act as a limiting factor in tree distribution.

Time factor

The time factor deserves a most important place in any consideration of the distribution of forest trees, and it is of particular significance in connection with the forests of Ontario. Time as a

factor in limiting the distribution of forest species is an expression of the rate of change in ecological conditions and of the specific rates of migration of the various species. Ordinarily conditions change so slowly that migration keeps pace; when there are more rapid changes migration lags behind. The time factor, therefore, must be considered in relation to the rate of change of such conditions as temperature, water, soil, light intensity, and secondarily in relation to methods of distribution.

WARMING (24) states, "Changes in the physical relationship of the soil are everywhere and always taking place, and in close correlation with this plant communities also undergo modification, but it does not seem possible to use development as the fundamental basis of classification of plant societies." COWLES (7), while recognizing the same factors, attaches more importance to development of successional associations.

The forests of Ontario have been made possible only by the retreat of glacial ice and water and the establishment of conditions permitting the growth of trees. It is evident that modifications of temperature have been prerequisite for the northward migration of tree species; by many it is regarded as the only factor. ADAMS suggests that the northern migration following the retreating glacier would comprise 3 great waves of life: (1) a wave of glacial or arctic vegetation, of which there are remnants in New York and Mount Marcy and two or three other high peaks; (2) a wave comprising the northernmost species of trees, stunted willows, birches, alders, and the coniferous forest spruces, hemlock, and pines; (3) a wave embracing the temperate zone deciduous trees. HARSHBERGER records a similar conclusion: "Several great waves of plant migration may be recognized, namely, glacial vegetation, tundra coniferous forests, and a migration of the deciduous forest elements from the southeastern center." If forest migration has kept pace with temperature changes, it might be expected that the limits of forest species would conform in outline with respective isotherms. It has already been demonstrated that in many instances this is not the case. The conclusion that in many places the migration of such species as *Tsuga canadensis*, *Acer saccharum*, and *Fagus americana* has lagged behind temperature changes is

made necessary. To a greater or less extent this is true of all the species forming the forests of Ontario. Under existing temperatures any further migration is dependent upon changes in the conditions now acting as limiting factors, as water, soil, and light. The rate of migration, and hence the distribution of forest trees, is dependent, primarily, upon the rate of change in temperature; however, migration may be restricted by other factors.

There is reason to believe that the yearly precipitation has gradually decreased since the glacial epoch. The data regarding the exact extent of these changes are limited. There can be no doubt, however, that the westward migration made possible by temperature changes has been checked by the water factor; also the irregularity of the limits of *Pinus Banksiana* may be explained by the fact that although temperature conditions have so changed that this species has migrated to 56° N. lat. in the highlands of northern Quebec, it has been limited in its northward progress by the low lying lands south and westward from James Bay. The inconsistencies of data regarding the northward distribution of *Pinus Banksiana* are doubtless due to the presence of certain outliers which might be expected when available soil moisture and other soil conditions act as the limiting factor, but which would be most improbable were temperature the determining factor of distribution. In regions where water is a limiting factor the rate of migration is dependent upon the rate of change in water conditions, in other words, upon the time factor.

Time factor in relation to soil development

It has been demonstrated that soil development, particularly with reference to the humus content, is a potent factor in determining the boundaries separating the *Acer-Fagus* and the *Abies-Picea* forests of Ontario. Since the *Acer-Fagus* forest demands the most highly developed soil, we are forced to the conclusion that in a forest succession the deciduous hardwood forest is the climax type. Over a vast area this climax type of forest has been excluded by soil conditions rather than by temperature. Northward migration of the deciduous hardwood forest has been limited by the rate of soil changes rather than by the rate of temperature

changes; with respect to the latter migration has lagged behind. Upon such a basis the "anomalous" separation of the deciduous hardwood forest and the coniferous forest is readily explained. The granitic rock of the Laurentian Plateau has weathered slowly, humus has accumulated slowly; in brief, the soil has developed slowly, hence the migration of the climax forest has been checked. This principle applies regionally as well as locally. In the region of glacial moraines the deep soil has made possible a rapid accumulation of humus, as well as a thorough intermingling of rock soil and humus. There has been a rapid development of the soil, consequently the *Acer-Fagus* forest has been permitted to invade such regions. The time factor as an expression of the rate of soil development has limited the rate of migration and hence forest distribution also.

The time factor in relation to soil development explains both the numerous northerly outliers of *Acer* associations and also the outliers of the *Picea-Abies* forest. The northward deviation of the limits of such species as *Acer saccharum*, *Fagus americana*, and *Tsuga canadensis* has been noted. It is significant that this deviation coincides with a great depression extending to the height of land in which highly developed soil deposits are present. The deciduous hardwoods occur as outliers and are always found on the better soils. Although the writer has not been able to study the Saugenay basin personally, it may be ventured that the northward migration of *Acer* at this point is also to be explained on the basis of soil development. BRAY (5) has found difficulty in explaining the occurrence of such trees as *Abies* and *Picea* in the swamps of New York. The soil in such localities is in a primitive stage of development. Although much humus has accumulated, there has been little or no intermingling of rock soil and humus, and the degree of aeration is low. The soil has been protected from the action of atmospheric agencies and running water, hence its undeveloped condition. The result is the same as when the slowly weathering Laurentian rock resists the agencies which promote soil formation. The fact that the same forest species are present in both places emphasizes the potency of the rate of soil development as a factor in the determination of tree distribution.

The evidence submitted is regarded as sufficient to prove that throughout a great region of Ontario dominated by *Picea* and *Abies* these genera are not permanent or climax forms, since they are replaced by *Acer* when soil conditions become favorable. WHITFORD (25), after studying the forests of Michigan, states that soils are improved by coniferous trees, and when sufficient humus soil has accumulated the deciduous species establish themselves. BRAY (5) also implies this relation. COOPER (6), however, after a study of Isle Royal, comes to the conclusion that "this type (*Abies-Picea-Betula* forest) is the climax forest of that portion of the northeastern conifer region under consideration; in other words, upon Isle Royal it is the final and permanent vegetative stage toward the establishment of which all other plant societies are successive steps. It is the climatic forest of the region, permanent while the climate remains essentially as now." The same paper records stands of *Acer* on certain ridges of Isle Royal and in other places where soil conditions seem particularly favorable. It seems probable that the occurrence of these stands might be explained on the basis of soil development.

It is evident from a study of the forests of northern Ontario that the deciduous hardwood forest is encroaching upon the coniferous forest region, and that the progress of this encroachment has lagged behind temperature changes, being now dependent principally upon the rate of soil development.

The relation of shade to the time factor of distribution is in accord with the specific tolerance of a given species with respect to light. The *Acer-Picea* forest provides shade which is essential for *Acer* seedlings, while detrimental to *Picea* or *Abies* seedlings. The encroachment of the deciduous hardwood forest upon the coniferous forest, made possible by changes in temperature and soil development, is also promoted, and the result made more permanent by decreasing light intensity due to shade conditions.

The importance of methods of seed dispersal as an element of the time factor of distribution is obvious. Where changes in conditions are slow, for instance yearly temperature modifications, even the trees whose methods of dispersal allow them to migrate slowly

are able to keep pace, and where ecological changes are more rapid species having the best methods of seed dispersal naturally migrate most rapidly. The rapid invasion of a burned area by the *Populus-Betula* association is due primarily to the widespread dispersal of the seeds of these species. In contrast, *Pinus* takes its place among the trees which appear later, largely because it has a less efficient method of scattering seeds. A number of examples of the limitations of seed dispersal have been noted. In several cases where a burn had left only one or two pines upon an island the usual *Populus-Betula* association was unable to gain a foothold because of the distance from the mainland; hence these species were superseded by numerous pine seedlings. Doubtless the same principles may be applied to the relation between seed dispersal and tree migration even over greater areas. The time factor of distribution may be an expression of the rate of migration as it is determined by the method of seed dispersal.

The time factor of distribution is an expression of the rate of migration. The rate of migration is dependent upon such primary conditions as temperature, water supply, soil properties, light intensity, and methods of distribution. Time, as a condition of change in environmental factors, becomes itself of great importance in any consideration of the factors of forest distribution.

Competition factor

Competition results in the survival of the fittest. The fittest is that species or individual whose specific range of tolerance is best related to the environmental condition acting as a limiting factor toward other species; hence temperature, water supply, soil, or light may act as the basis of competition. Time may also act as a basis of competition, since it changes conditions in environmental factors. In order that competition may act as a distributional factor, conditions must be favorable for one or more species and unfavorable for others. While the time factor is an expression of the rate of change of the environmental factor acting in a limiting capacity, the competition factor is an expression of the relation between the ranges of tolerance of the forms in question toward the limiting environmental factor.

The encroachment of the deciduous hardwood forest of Ontario upon the coniferous forest is accompanied by competition. The progressive changes in such conditions as humus content of the soil and light intensity are such as to increasingly favor the former association to the detriment of the latter. *Abies*, for instance, grows readily on good soil, but it cannot tolerate the shade of an *Acer* forest. The competition becomes too great; in other words, the changes in environmental factors have been such that the mean of the range of tolerance of *Acer* more closely approximates existing conditions than that of *Abies*. The factor of competition plays its chief rôle in the so-called transition areas, where the specific ranges of tolerance of the species concerned all include existing conditions although unequally. That species dominates, other things being equal, whose mean of tolerance more nearly approximates environmental conditions.

Specific ranges of tolerance

The specific ranges of tolerance of some of the dominant forest species of Ontario, together with their relation to limiting factors, will be considered. Many of the data are represented diagrammatically in the accompanying diagrams (figs. 3–6). These diagrams summarize data collected regarding the specific ranges of tolerance of a number of forest species. In preparing the temperature diagrams (fig. 3), for example, other factors have been eliminated by selecting data respecting localities where other conditions have been favorable; in this way the maxima and minima have been determined. The diagrams are relative rather than quantitative, hence they suggest a field of research which would supply absolute numbers. When the maxima and minima have been determined, the means are represented by the mid-points of the lines joining these extremes. The radii of the circles of which the lines joining the extremes are diameters represent the magnitudes of the specific ranges of tolerance. The comparative areas of distribution as determined by the several limiting factors are represented, theoretically, by circles whose centers are the means of their ranges of tolerance and whose radii are the lines representing those ranges.

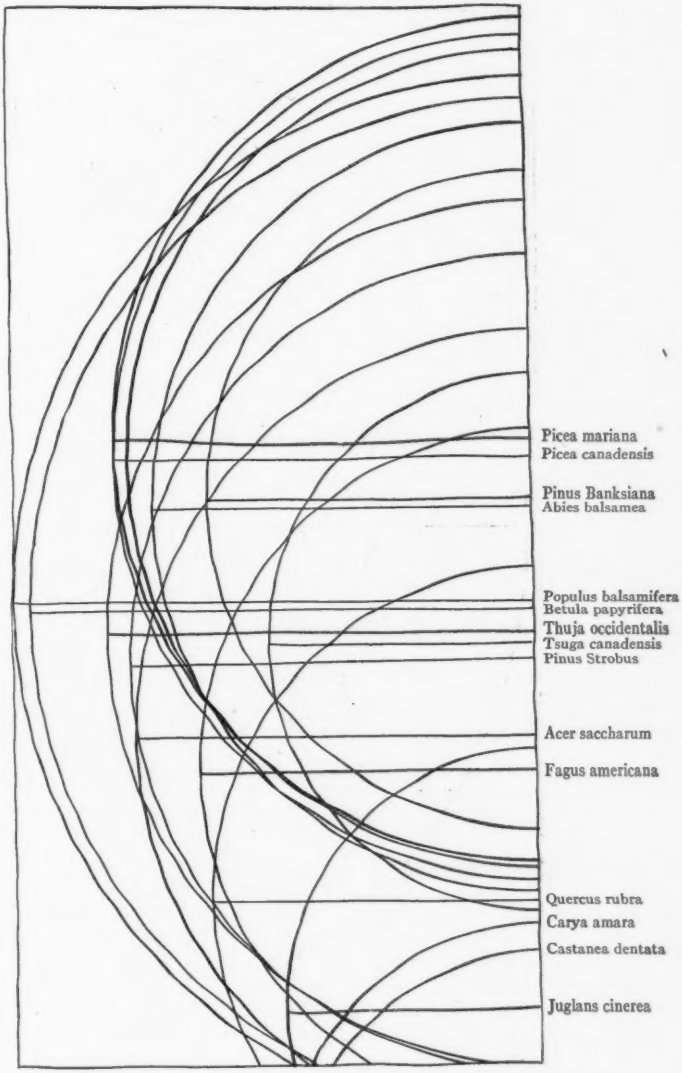

FIG. 3.—Forest trees: specific ranges of tolerance with respect to temperature

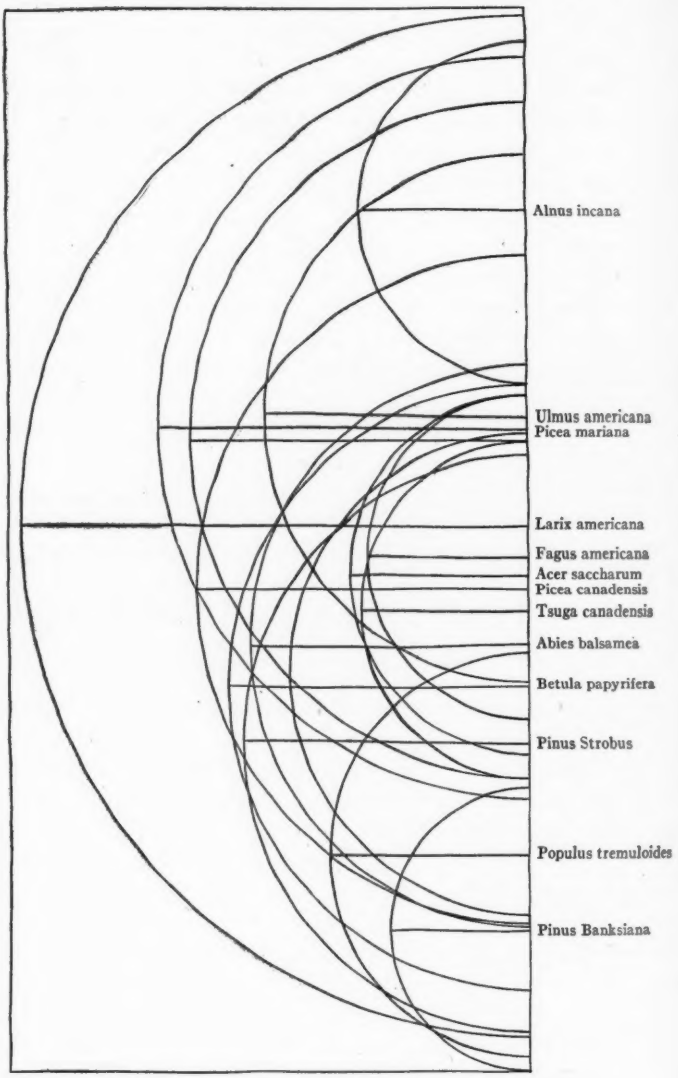

FIG. 4.—Forest trees: specific ranges of tolerance with respect to water

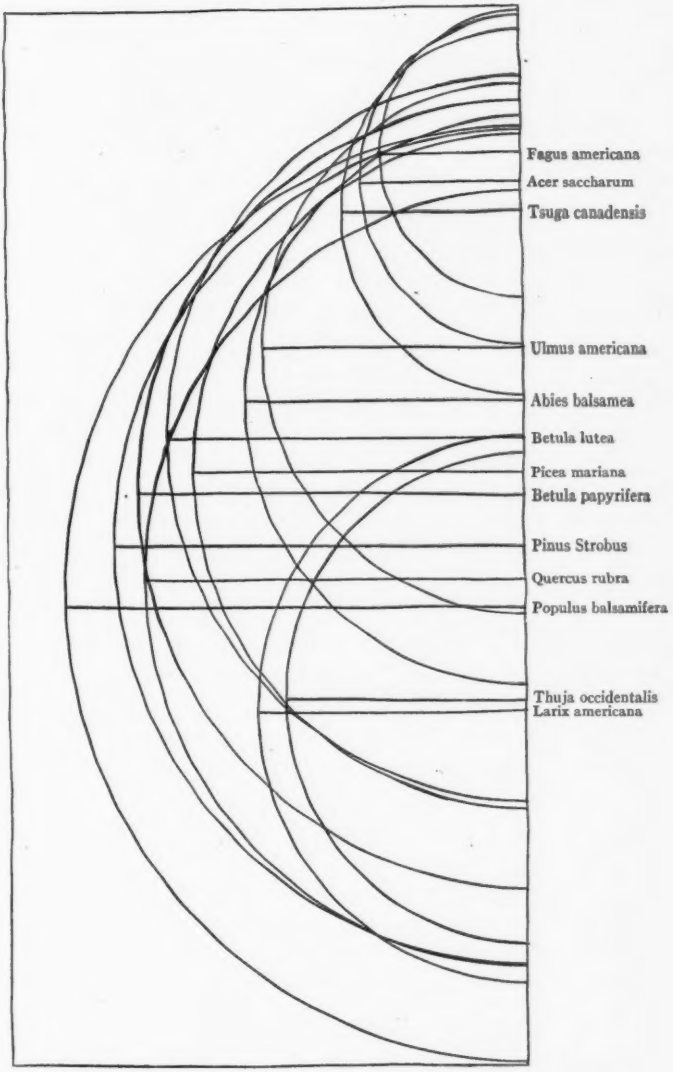

FIG. 5.—Forest trees: specific ranges of tolerance with respect to soil development

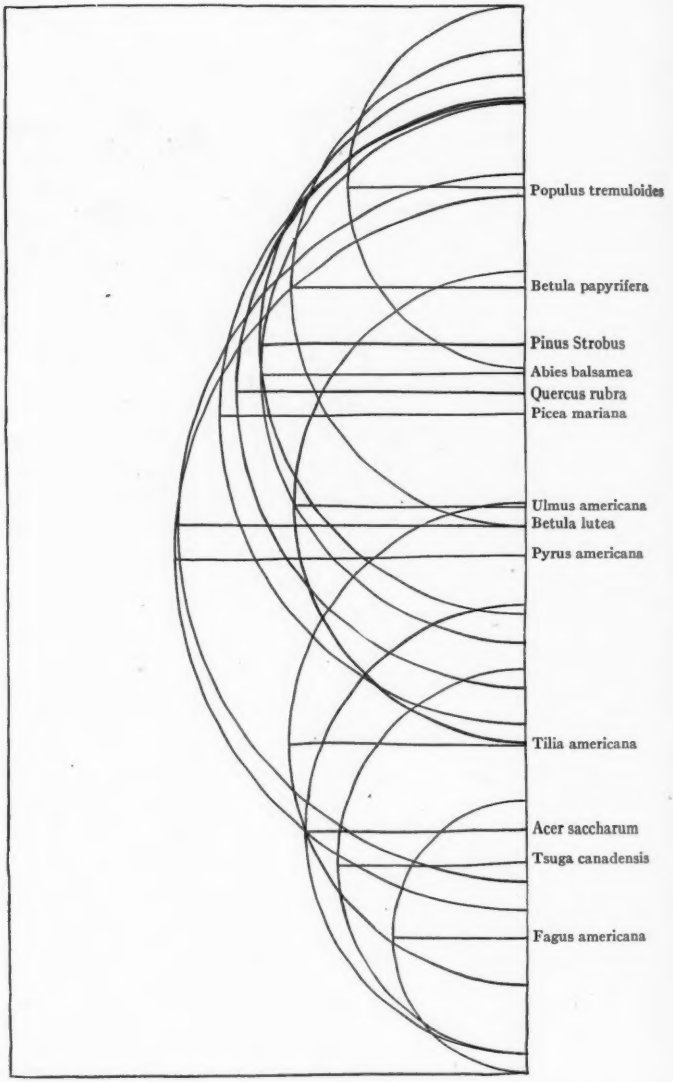

FIG. 6.—Forest trees: specific ranges of tolerance with respect to intensity of light

ABIES BALSAMEA.—*Physical factors.*—"Moisture and temperature are the main factors influencing the distribution of *Abies balsamea;* it requires a cold climate and a constant supply of moisture at its roots; a mean annual temperature not exceeding 40° F. with an average summer temperature of not more than 70° F. and a mean precipitation not less than 25 inches evenly distributed throughout the year are the necessary conditions for its growth" ZON (27). The maximum of its range of temperature tolerance is high, very closely approximating that of *Picea;* the minimum is lower than has generally been conceded, other factors having practically eliminated it from the warmer regions of its normal temperature range. While *Abies balsamea* normally has a wide water range, it seldom thrives except in a moist soil because this hinders the growth of a fungus which in a drier soil attacks the roots ("ground rot"). Southward *Abies balsamea* "attains its best growth and largest sizes on flats the soil of which is usually a moist deep sand loam" (ZON 27), while "southwest of Hudson Bay it grows only in the warmest and best soils and is entirely wanting in the cold swampy tracts" (LOW 18). *A. balsamea* demands comparatively high light intensity; seedlings are seldom found except in clearings caused by windfall, or otherwise. Generally, *Abies* has a wide range of tolerance.

Competition factor.—Northward *Picea* is the chief competitor of *Abies;* their ranges of tolerance are similar, the maxima and minima of *Picea* generally being more extreme; consequently *Abies* under most conditions would be secondary were it not for the fact that near the mean of their ranges *Abies* grows more rapidly than *Picea.* Southward the chief competitors are *Acer* and *Tsuga.* These forms have the advantage of being more shade tolerant, and hence they gradually encroach upon and finally exterminate *Abies,* which demands greater light intensity (fig. 7).

Time factor.—The northward migration of *Abies balsamea* is conditioned by temperature, and since the magnitude of temperature changes is dependent upon time, it is evident that the time factor has a bearing upon distribution. The distribution southward is affected by competition of such forms as *Acer* and *Tsuga.* Time is necessary for the environmental changes which produce

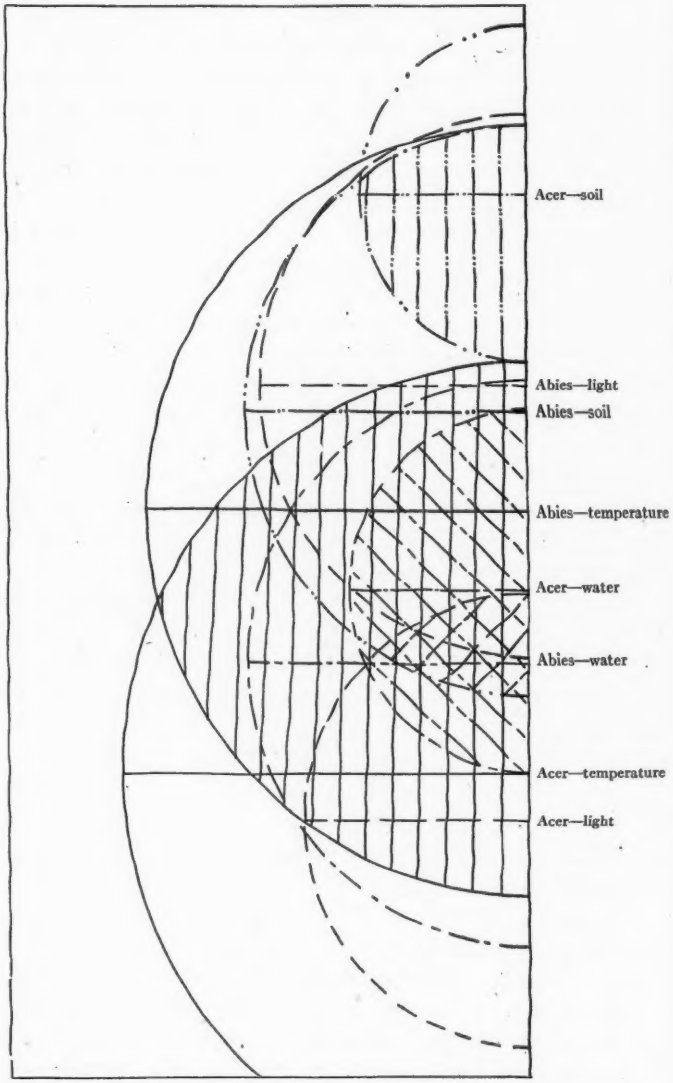

FIG. 7.—Competition areas of *Abies balsamea* and *Acer saccharum* shown by superimposing specific areas of tolerance toward factors of temperature, water, soil, and light; overlapping areas barred, the bars being similar to radii representing ranges of tolerance; barred areas represent areas of competition.

conditions more nearly approximating the mean of the range of tolerance of these competitors, thereby contributing toward the elimination of *Abies*.

The problem which arises by the appearance of *Abies* in swamps south of its "normal" range may be explained by regarding soil rather than temperature as the limiting factor. Soil changes have been slower in the undisturbed humus and rock soil layers of the swamp than on the weathered uplands. Soil conditions approximating the mean of the range for *Abies* have been maintained, hence this form has persisted; also, the presence of abundant water inhibits the attacks of parasitic fungi, thereby permitting the growth of *Abies*.

PICEA MARIANA AND P. CANADENSIS.—Although these species are closely related morphologically, they are quite different ecologically; in this respect *P. canadensis* is quite closely associated with *Abies balsamea*. *P. mariana* has a wider range of tolerance than either. Low states, "In Labrador (and northern Quebec) the white spruce grows on rich intervale grounds or near the shores of lakes and rivers. The black spruce is found on hills and in cold swamps. The two kinds have the same geographical range northward." Soil development and soil water frequently become limiting factors, separating these species. The status of temperature as a factor in distribution is demonstrated by the differences existing between *Picea mariana* and *P. canadensis*. Although they have practically the same temperature range, the latter is not found throughout a vast area of the region lying between Hudson Bay and Labrador. Available accounts and the evidence given by its habitat in other regions indicate that soil development is the limiting factor. In this respect *Abies balsamea* takes a position intermediate between these two species of *Picea*. *Picea* has previously been referred to as the chief competitor of *Abies*.

LARIX AMERICANA.—This species has a very wide range of tolerance toward temperature, water, and soil conditions. BELL (2) states "That it has an equally thrifty growth in the country to the south of James Bay and westward toward Lake Winnipeg. In this great region it attains its greatest perfection in the dry uplands and in good soil near the rivers, but smaller trees with small

black spruces grow everywhere on the low swampy grounds. South of the Ottawa River it grows principally on low and level land." Low states, "*Larix* is probably the hardiest tree of the subarctic forest belt. Throughout the interior it is found in all the cold swamps and is always the largest tree in the vicinity. Along the northern margin of the forest the larch continues a tree to the very edge where the black spruce is dwarfed to a mere shrub. *Larix* demonstrates the principle that a tree which has a wide range of tolerance does not flourish in competition with species of smaller range, but is crowded into situations where conditions exclude competitors. Such a form is usually of slow growth compared with forms which are more specialized. *Larix* cannot be called a xerophyte, a hydrophyte, or a mesophyte, since it may be any of the three. Although it is usually found under extreme conditions, it grows best under mean conditions, provided competitors have been eliminated. The distribution of *Larix* is accounted for by its wide range of tolerance, together with its low status in the competition scale."

THUJA OCCIDENTALIS.—The "anomalous" distribution of *Thuja occidentalis* defies explanation by regarding temperature, water, or soil as the limiting factors (figs. 1, 2). "It is absent in Newfoundland, Cape Breton, Nova Scotia, and the east half of Prince Edward Island, but unusually large and fine in New Brunswick and the Gaspé peninsula, in which the climate, soil, etc., are the same as in the adjacent regions, where no trace of the species is to be found." BELL (2) also states that "there is a remarkable outlier of white cedar brushwood around Cedar Lake on the upper part of the Saskatchewan River at a distance of 190 miles to the northwest of the nearest point of the main area covered by this species." Moreover, it is notable that throughout great areas, for instance the Temagami region, *Thuja* is unknown, while in the surrounding country it is abundant. *T. occidentalis* has a wide range of tolerance toward environmental conditions. The presence of "outliers" where conditions are similar to those prevailing in other regions where it ordinarily occurs indicates that the general area of its distribution does not extend to its ecological limit, in many instances at least. The northern area of its distribution is

roughly outlined by a semicircle, a fact which contributes evidence that *Thuja* has migrated radiately from a limited area. The method of reproduction is such that it does not migrate rapidly; that a great proportion of seeds fail to develop is of importance in this connection. It would seem that the migration of this form has lagged behind changes in ecological conditions. With respect to its range of tolerance and its position in the scale of competitors under mean conditions, *Thuja* resembles *Larix*. These characters, together with the limiting action of time, account for most of the facts of its distribution.

PINUS BANKSIANA.—The tolerance of this form toward low temperatures, dry conditions, and soil poor in humus, together with its limited range toward the other extremes, place it in a unique place among the trees of the northwestern region. It is practically eliminated from the low lying lands to the south and west of Hudson Bay and James Bay, water being the limiting factor. The inconsistencies in accounts of its northward distribution in this region are the result of its occasional presence where there are higher lands between rivers. It extends northward to 56° N. lat. on the dry uplands east of Hudson Bay. Farther south, also, it is to be found only on dry rocky or sandy soil containing little humus. It is one of the pioneer forms and survives where it can avoid competition by enduring severe conditions.

PINUS STROBUS.—This species is also a pioneer among the conifers. Seedlings are seldom found except where there is a high light intensity and well drained soil. Its ranges of tolerance with respect to temperature and water do not include the extremes which characterize *P. Banksiana*. The northern limit follows a yearly isotherm (33° F.) very closely. It would seem that in this case temperature acts as a limiting factor. Because of its longevity and its towering height individuals or groves of mature trees often persist in a region where seedlings have long been eliminated by other forms which are higher in the competition scale. The pine forest is normally succeeded by such forms as *Tsuga* or *Acer* whose seedlings tolerated shade, the time factor; hence its perpetuation depends upon the maintenance of or reversion to pioneer conditions.

TSUGA CANADENSIS.—This species is among conifers what *Acer* and *Fagus* are among deciduous trees; it is a climax form. In fact, its ranges of tolerance are almost identical with those of the deciduous forms already mentioned. *T. canadensis*, when contrasted with such species as are represented by *Pinus Banksiana*, serves to emphasize the ecological diversity of conifers. BELL (2) states that "this tree maintains a good size to the verge of its range and always appears to terminate abruptly." Stands of mature trees are to be found as "outliers" beyond the general area of its distribution. This evidence confirms the belief that *Tsuga* is still migrating; that in many instances it has been limited by the time factor rather than by environmental factors.

POPULUS BALSAMIFERA AND P. TREMULOIDES.—Although *P. balsamifera* generally extends farther north than *P. tremuloides*, having a greater temperature range of tolerance, its northern limit passes south of the latter at 71° W. long.; soil becomes the limiting factor in this region. *P. balsamifera* "appears to confine itself to heavy clay soil of the river valleys on the modified drift of the Cambrian areas" (LOW 18), while "*P. tremuloides* is most plentiful on the unmodified glacial till of the drift ridges." The seedlings of both require a high degree of light intensity, and as such are pioneer forms. Southward they occur only where fire and other destructive agencies have restored pioneer conditions. The abundance of these species of *Populus* northward, especially south and west from Hudson Bay, would indicate that this region is biologically young.

ACER SACCHARUM.—South of the Laurentian Plateau *A. saccharum* dominates, except in the undrained lowlands. Its range of tolerance is limited to a mature soil (that is, well drained, well aerated, and containing a relatively large amount of humus intimately mixed with the rock soil) and low light intensity. The humidity of the atmosphere in Ontario is such that it is doubtful whether it ever acts as a limiting factor, other conditions being favorable. It is evident that the distribution of *Acer* is chiefly an expression of the time factor; the time required to give rise to a deep, well drained humus soil and to shade conditions, and in addition the time which is necessary to crowd out those forms which

have been instrumental in providing such conditions. As mentioned before (under time factor), the time rate of change has been less in the lowlands and upon the rock outcrops of the Laurentian Plateau than upon the highland and the weathered glacial moraine. There is abundant evidence that *Acer* is migrating northward, its progress being contingent upon the time rate of soil development.

FAGUS AMERICANA.—This species has a range of tolerance toward soil conditions which is even more limited than that of *Acer*. What has already been said for *Acer* applies equally for *Fagus*, since the latter is closely associated with the former.

ULMUS AMERICANA.—This species is another form whose distribution defies explanation by considering either temperature or rainfall as limiting factors. The limit extends well into the plains and northward beyond Lake Winnipeg; it swings southward, then northward again in the region south of James Bay; then abruptly southward and again northward with no apparent dependence upon temperature or precipitation conditions. Even within its general limits it is found only where there is a clay, imperfectly drained soil; over large areas, especially throughout the Laurentian Plateau, it has not been found. "On the Missinabi or west branch of the Moose River the white elm reappears 130 miles north of its general boundary on descending to a sufficiently low elevation above the sea" (BELL 2). Soil conditions are the chief limiting factors; on the clay soil of the lowlands, where there is poor drainage, is its favorite habitat; for this reason it is intermittingly distributed. Its reappearance north of the height of land, its occurrence in the lowlands about Lake Winnipeg, as well as many other eccentricities of this species, may be explained upon this basis.

BETULA LUTEA.—This species may be associated with pioneer forms such as *B. papyrifera* or climax forms such as *Acer*. "Yellow birch is the most abundant hardwood in New England" (12), while in the lake region it is seldom seen; it becomes more abundant in the Laurentian region. "It grows in forests of widely different composition and shares to some extent the habits of paper birch, appearing on burns in small even-aged stands" (12). The seedlings are pioneer, yet, because of its comparative longevity,

the species persists after such forms as *Picea*, *Abies*, and even *Acer* have established themselves. Among such forms only mature trees are to be found. These characters explain its distribution. In New England and the Laurentian region the time rate of change has been small. The forms which will eventually succeed this species have not had time to eliminate it. On the glacial moraine of the lake region this process of crowding out has in most places reached completion.

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NOTES ON NORTH AMERICAN TREES. III. TILIA. II

C. S. SARGENT

8. TILIA NEGLECTA Spach, Ann. Sci. Nat. II. 2:140, *t. 15.* 1834; Hist. Vég. 4:29. 1835.—*Tilia americana* Curtis, Rep. Geol. Surv. N. Car. 3:79 (not Linnaeus). 1860; *Tilia pubescens* Watson and Coulter, Gray's Man. ed. 6, 71 (in so far as relates to Long Island) (not Aiton). 1889; Sargent, Silva N. Am. 1:55 (in so far as relates to Long Island). 1891; Robinson, Gray Syn. Fl. 1¹:343 (in so far as relates to Long Island). 1897; Britton and Brown, Ill. Fl. 2:414 (in so far as relates to Long Island). 1897; *Tilia Michauxii* Sargent, Man. 673. *fig. 549* (not Nuttall). 1903; Robinson and Fernald, Gray's Man. ed. 7. 565. 1908; Britton and Brown, Ill. Fl. ed. 2, 513 (probably in part). 1913.—Leaves thick and firm, acute or abruptly narrowed and long-pointed at apex, obliquely concave or unsymmetrically cordate at base, coarsely serrate with straight apiculate teeth pointing forward, dark green, smooth, glabrous and lustrous above, covered below except on the midribs and veins more or less thickly with short gray pubescence often slightly tinged with brown, and furnished with conspicuous tufts of axillary hairs, usually 11–14 cm. long and 6–11 cm. wide; petioles stout, glabrous, 3–6 cm. in length. Flowers about 1 cm. long, on pubescent or nearly glabrous pedicels, in long-branched, slender, glabrous, mostly 5–15-flowered corymbs; peduncles slender, glabrous, the free portion 3–4 cm. in length, the bract nearly sessile or raised on a stalk up to 1.5 cm. in length, gradually narrowed and cuneate or unsymmetrically cuneate or rounded at base, rounded at apex, glabrous, 1–2 cm. wide and 7–15 cm. long, longer than the peduncle; sepals broadly ovate, acute, ciliate on the margins, glabrous on the outer surface, covered on the inner surface with long white hairs, about half as long as the lanceolate petals, rounded and notched at apex and rather longer than the spathulate staminodia; stamens included; style villose toward the base. Fruit ellipsoidal, ovoid, obovoid, or depressed-globose, rounded or acute or rarely gradually narrowed

and acuminate at apex, rarely 5-angled, covered with rusty or pale pubescence, usually 8–10 cm. in diameter.

A tree 25–30 m. high, with a trunk sometimes 1 m. in diameter, smooth, often pendulous, branches forming a broad round head, and slender glabrous branchlets. Winter-buds ovoid, rounded at narrowed apex, about 5 mm. long, with glabrous, red-brown or light brown scales. Bark of the trunk about 2.5 cm. thick, deeply furrowed, pale reddish brown and covered with small thin scales. Flowers at the north in July and southward about a month earlier. Fruit ripens in September.

Rich moist soil, Province of Quebec, near Montreal, to the coast of Massachusetts and New York, through the middle states to the valley of the Potomac River and along the Appalachian Mountains to those of North Carolina, and to Iuka, Tishimingo County, Mississippi, and from central and western New York to northern and southwestern Missouri (*B. F. Bush*, Noel, May 27 and October 8, 1909, nos. 5765, 5983; *E. J. Palmer*, Elk Springs, McDonald County, no. 4285; limestone cliffs, Current River, Van Buren County, July 4, 1914, no. 6180).

Although I have not seen a type specimen of SPACH'S *T. neglecta*, his description can only refer to this tree, which seems to have been understood only by SPACH, whose description was made from trees cultivated in France. The younger MICHAUX must have seen it in western New York, where he found what he called *T. americana* between Batavia and New Amsterdam forming two-thirds of the forest growth. In western New York, however, *T. neglecta* is a much more common tree than *T. glabra*. GRAY, too, must have been familiar with *T. neglecta*, for it is common in central New York where as a young man he did most of his field work, and in his descriptions of *T. americana* he always says "essentially glabrous," which would indicate that it might not be always glabrous. It was mistaken for *T. glabra* by CURTIS as it seems to replace that species south of Maryland. Specimens of a tree of *T. neglecta* growing near Wading River, Long Island, have been referred by many authors to *T. pubescens* Aiton, and other authors have followed me in considering the tree which I now consider *T. neglecta* to have been the *T. Michauxii* of NUTTALL, which is the *T. argentea* of MICHAUX.

In the shape and serration of the leaves and in the size and structure of the flowers and fruit there is little by which *T. neglecta* can be distinguished from *T. glabra*, but as the absence or presence of pubescence or tomentum on American species of *Tilia* is so important in distinguishing species, and as the pubescence on the lower surface of the leaves of *T. neglecta* is so constant and so persistent throughout the season, it seems best to consider it a species rather than a pubescent form of *T. glabra*. The base of the style of *T. neglecta* is furnished with long hairs and that of *T. glabra* appears to be quite glabrous. I find a slight pubescence on a branchlet from the upper part of a tree collected by CURTIS and COIT near Ithaca, New York. SPACH describes the fruit of

his species as subpentagynous, and his figure represents a fruit with 5 distinct ridges. I have not seen such fruits on any specimens of wild trees, but they occur on two specimens of cultivated trees in the herbarium of the Arboretum, one from Germany and the other from Rochester, New York. On a tree cultivated in Goldsboro, North Carolina, the fruit is ellipsoidal and borne in unusually long-branched clusters.

9. TILIA CAROLINIANA Miller, Dict. ed. 8. 1758.—*Tilia pubescens* Aiton, Hort. Kew. 2:229. 1789; Ventenat, An. Hist. Nat. 2:68. 1800; Mém. Acad. Sci. Paris 4:10. *t.* 3. 1802; Elliott, Sk. 2:3. 1824; *Tilia multiflora*, Hort. ex Ventenat in An. Hist. Nat. 2:64. 1800; *Tilia pubescens* var. *leptophylla* Ventenat, *l. c.*; *Tilia leptophylla* Small, Fl. Southern States 762 (in part?). 1911.—Leaves ovate, oblique and truncate or cordate at base, abruptly long-pointed at apex, coarsely dentate with broad apiculate glandular teeth pointing forward, and coated below with a rusty or pale easily detached pubescence of fascicled hairs; when they unfold coated with hoary tomentum, soon glabrous on the upper surface, and at maturity dark yellow-green and lustrous above, 7–15 cm. long and 6–12 cm. wide; petioles stout, glabrous, 2.5–4 cm. in length. Flowers 6–7 mm. long, on slender pubescent pedicels, in small stout-branched, pubescent, mostly 8–15-flowered corymbs; peduncle slender, pubescent, the free portion 2–3 cm. long, the bract nearly sessile, oblong-obovate, cuneate at base, rounded or acute at apex, when it first appears nearly glabrous on the upper surface, pubescent becoming glabrous or almost glabrous below, 2 cm. wide, longer or shorter than the peduncle; sepals ovate, acuminate, ciliate on the margins, brown and covered with pale pubescence on the outer surface, coated on the inner surface with long white hairs; petals lanceolate, acuminate, a third longer than the sepals; staminodia oblong-obovate, rounded at apex, rather shorter than the petals; style tomentose at base or glabrous. Fruit subglobose, ellipsoidal or obovoid, 7–9 mm. in diameter.

A large tree with slender, red-brown, glabrous or slightly pubescent branchlets. Winter-buds ovate, acute, glabrous or rarely pubescent, 5–6 mm. long.

NORTH CAROLINA.—Wrightsville Beach, New Hanover County, *W. W. Ashe* (no. 261); Wilmington, New Hanover County, *T. G. Harbison*, June 21, 1915, May 2, 1916 (nos. 6, 8, 11, 12).

SOUTH CAROLINA.—Near Charleston and on James Island, *T. G. Harbison*, June 17 and 18 and September 6, 1915 (nos. 1, 7, 8, 13, 14, 14a), September 4 and 5, 1916 (nos. 15, 17, 18), May 1, 1917, June 3, 1918 (nos. 45, 46, 47, 48); Calhoun Falls, Abbeville County, May 26, 1918 (no. 17).

GEORGIA.—Colonel's Island, near Dunham, Liberty County, *T. G. Harbison*, September 8 and 9, 1916 (nos. 3, 7), June 19, 1917 (no. 18), *Miss Julia King*, October 1917.

LOUISIANA.—Avery Island, Iberia Parish, *R. S. Cocks*, October 18, 1910 (no. 6), May 24, 1914, May 29, July 28, 1916 (nos. 4040, 4054), *Miss McIlhenny*, June 1915; Welsh, Jeff Davis Parish, *E. J. Palmer*, May 17, September 10, 1915 (nos. 7675, 8494); Opelousas, St. Landry Parish, *C. S. Sargent*, March 25, 1917; Little Bayou Têche, east of Opelousas, *R. S. Cocks*, April 3, July 24, 1916 (nos. 4012, 4016, 4018); rich woods near Winnfield, *C. S. Sargent*, April 6, 1913; Lake Charles, Calcasieu Parish, *C. S. Sargent*, April 10–13, 1915, *R. S. Cocks*, May 21, June 1, 1915 (no. 2530); Natchitoches Parish, Natchitoches, *R. S. Cocks*, April 15 and 27, 1911, *E. J. Palmer*, April 17 and 23, May 3, June 10 and 14, July 10, September 30, 1915 (nos. 7397, 7474, 7946, 7952, 8013, 8021, 8747, 9416); Creston, *E. J. Palmer*, April 28, 1915 (no. 7420); Chopin, May 6, 1915 (no. 7554).

ARKANSAS.—Fulton, Hempstead County, *B. F. Bush*, October 4, 1909 (no. 5926); Gum Springs, Clark County, *E. J. Palmer*, June 20, 1915 (no. 8074).

TEXAS.—Palestine, Anderson County, *E. J. Palmer*, September 21, 1917 (no. 12816); Marshall, Harrison County, June 8 and September 26, 1915 (nos. 7910, 8673), March 29, 1918 (no. 1320); Groesbeck, Limestone County, June 1, 1915 (no. 7934); Jacksonville, Cherokee County, June 4, 1915 (no. 7871); Larissa, Cherokee County, April 7, 1916 (nos. 9374, 9381); Houston, Harris County, September 15, 1917 (no. 12759); San Augustine, San Augustine County, April 19 and September 8, 1916 (nos. 9498, 10637); near Pledger, Matagorda County, May 8, 1916 (nos. 9698, 9704); Dayton, Liberty County, May 25, 1915 (no. 7767); Blanco, Blanco County, June 4, 1917 (no. 12165); near Boerne, Kendall County, *S. H. Hastings*, 1911, *C. A. Schattenberg*, 1915, *C. S. Sargent*, 1915, *E. J. Palmer*, September 29, 1916 (no. 10866), April 20, 1917 (no. 10866).

MEXICO.—Botteri, "998 Juni 55, Orizaba" (in Herb. Kew), Orizaba, 63, 1869 (in Herb. Kew), Pr. el Chica, *C. Erenberg* (in Herb. Kew, with slightly pubescent branchlets and winter-buds).

MILLER's specimen of his *T. caroliniana* from a tree cultivated in England, where it had been introduced from Carolina by CATESBY, is preserved in the British Museum, the name being written on the sheet in MILLER's handwriting. This specimen is also the type of AITON's *T. pubescens*, that name also appearing on the sheet in AITON's or DRYANDER's handwriting. This specimen has glabrous branchlets, coarsely serrate leaves, very oblique and truncate at base, and covered below, like the corymbs, with rusty pubescence. The leaves are rather smaller than those of the trees now growing about Charleston Harbor,

as might be expected in the case of a tree from the southern states cultivated in England. There is no other linden in the South Carolina region which at all agrees with MILLER'S specimen, and his name can properly be taken up for this tree. *T. caroliniana* has usually been considered a synonym of *T. americana* Linnaeus, and *T. pubescens* has been adopted for one of the southern coast species. This name, however, except as a synonym of *T. caroliniana*, must now disappear.

The leaves of the specimens collected west of the Mississippi River which are here referred to *T. caroliniana* are certainly not thinner than those from the Carolina coast region, and I can find no characters by which the eastern and western trees can be distinguished. As here understood the range of *T. caroliniana* is remarkable, as there is no evidence that it occurs between the coast of Georgia and western Louisiana.

TILIA CAROLINIANA var. **rhoophila,** n. var.—*Tilia pubescens* Torrey and Gray, Fl. N. Am. 1:240 (insomuch as relates to Texas). 1842; *Tilia pubescens* Sargent, Silva N. Am. 1:55 (insomuch as relates to Louisiana and Texas). 1891, and later authors; *Tilia pubescens* var. a *Aitonii*, V. Engler, Monog. Tilia, 128 (insomuch as relates to Texas specimens). 1909.—Differing from the type in its pubescent branchlets and winter-buds, its usually larger leaves, and in its tomentose corymbs of more numerous flowers. Leaves broadly ovate, oblique and truncate or cordate at base, abruptly short-pointed and acuminate at apex, coarsely serrate with broad apiculate teeth pointing forward, dark green and lustrous on the upper surface, pale and thickly covered on the lower surface with persistent white or brownish pubescence, 10–12 cm. long and 7–12 cm. wide, with slender midribs and primary veins pubescent on the lower side and small conspicuous axillary tufts of pale hairs; petioles stout, thickly coated with pubescence, 2.5–4 cm. in length; on vigorous shoots leaves often 16 cm. long and 14 cm. wide, and occasionally 24 cm. long and 18 cm. wide. Flowers 5–6 mm. long, on short, hoary tomentose pedicels in wide, thin-branched, pubescent, many-flowered (sometimes 50) corymbs; peduncle thickly covered with fascicled hairs, the free portion 3.5–5 cm. long, the bract oblong, unequally rounded at base, rounded at apex, glabrous on the upper, pubescent on the lower surface, 1.5–2 cm. wide, usually shorter than the peduncle; sepals acuminate, coated on the outer surface with pale or slightly rusty pubescence, villose and furnished at base on the inner surface with tufts of long hairs; petals lan-

ceolate, acuminate and ciliate at apex, about a third longer than the sepals; staminodia spatulate, acute, about half the length of the petals; style coated at base with long white hairs. Fruit subglobose, covered with rusty tomentum, 7–8 mm. in diameter.

A tree with slender branchlets thickly coated during their first year with pale pubescence, dark red-brown or gray and puberulous during their second season. Winter-buds covered with pale pubescence.

ARKANSAS.—Fulton, Hempstead County, *E. J. Palmer*, June 17, 1915 (no. 8023); Gum Springs, Clark County, June 21, 1915 (no. 8074).

LOUISIANA.—Bank of the Calcasieu River, Lake Charles, Calcasieu Parish, *R. S. Cocks*, May 21, 1916 (no. 2532), *C. S. Sargent*, March 23, 1917; low woods, Welsh, Jeff Davis Parish, *E. J. Palmer*, May 17, June 21, and September 10, 1915 (nos. 7674, 8074, 8500).

TEXAS.—Houston, Harris County, *F. Lindheimer*, 1842 (no. 10830 in Herb. Missouri Bot. Gard.), *E. J. Palmer*, May 24 and 26 and September 17, 1915 (nos. 7758, 7776 type for flowers, 8578), April 29, 1916 (no. 9613), April 2, May 16, 17, 18 and September 15, 18, 1917 (nos. 11142, 11443, 11448, 11451, 11454, 11911, 11912, 11913, 11914, 11916, 11917, 11918, 11933, 11934, 11946, 11964, 12755, 12756, 12758, 12762, 12788), March 19, 29, 1918 (nos. 13114, 13115); Harrisburg, Harris County, *E. J. Palmer*, May 17, 1917 (no. 11933); Morgan's Point, Harris County, *E. J. Palmer*, May 20, 1917 (no. 11957); near Pledger, Matagorda County, *E. J. Palmer*, May 8, 1916 (no. 9695); Dayton, Liberty County, *E. J. Palmer*, May 25 and September 16, 1915 (nos. 7672, 7767, 7770, 8548, 8564, 8566), April 28, 1916 (nos. 9603, 9604, 9605, 9607), April 3, May 21, and September 17, 1917 (nos. 11457, 11458, 11460, 11465, 11466, 11975, 11976, 11982, 11984, 12776, 12777, 12778, 12779 with bracts of the peduncles 10–11 cm. long and 3.5 cm. wide); Palestine, Anderson County, *E. J. Palmer*, May 29, 1917 (no. 12086); Marshall, Harrison County, *B. F. Bush*, August 9, 1901 (no. 659), *E. J. Palmer*, June 8, 1915 (no. 7922); College Station, Brazos County, *E. J. Palmer*, April 28, 1917 (nos. 11720, 11721); Bryan, Brazos County, *E. J. Palmer*, April 28, 1917 (no. 11721); Liberty, Liberty County, *E. J. Palmer*, May 22, 1915 (no. 7735), April 28, 1916 (no. 9594); Livingston, Polk County, September 12, 1916 (no. 10697), September 19, 1917 (no. 12798); New Braunfels, Comal County, *F. Lindheimer*, 1842 (no. 10839 in Herb. Missouri, Bot. Gard.); rocky banks of the Guadalupe River, Kerrville, Kerr County, *E. J. Palmer*, April 29, 1916 (nos. 9931, 9934).

Growing usually on the margins of sandy bogs and on moist sandy hillsides, this tree varies, according to the moisture it obtains, in the size of the leaves and in the amount of the pubescence on the branchlets. The bark on trees growing in wet situations is smooth and pale, but on trees in dry soil or higher on the hillsides it is dark and rough; the leaves are smaller and the branchlets are less pubescent.

10. **Tilia texana**, n. sp.—*Tilia pubescens* var. *β Ventenatii* V. Engler Monog. Tilia 129 (in part). 1909.—Leaves thin, oblong-ovate, abruptly contracted into long slender acuminate points, cordate or obliquely cordate at base, finely dentate with broad apiculate teeth; early in the season pubescent above with scattered fascicled hairs and covered below with brownish, slightly attached pubescence, and in the autumn light yellow-green, lustrous and nearly glabrous on the upper surface, slightly pubescent on the lower surface, 10–14 cm. long and 8–10 cm. wide, with slender midribs and primary veins sparingly villose on the upper side and nearly glabrous on the lower side, and small axillary tufts of brownish hairs; petioles slender, pubescent with fascicled hairs, 2.5–4 cm. in length; leaves on vigorous shoots often furnished with one or two large, lateral, acuminate, serrate lobes, more coarsely dentate and more thickly covered on the lower surface with pubescence, often 13–15 cm. long and 9–15 cm. wide. Flowers 6–7 mm. long on slender tomentose pedicels in small, villose-pubescent, mostly 7–10-flowered corymbs; peduncle slender, slightly villose-pubescent, the free portion 3–3.5 cm. in length, the bract oblong-ovate to slightly obovate, unsymmetrically cuneate at base, rounded and occasionally lobed at apex, glabrous on the upper surface, densely pubescent early in the season, later becoming nearly glabrous on the lower surface, longer or shorter than the peduncle; sepals ovate, acute, pale pubescent on the outer surface, covered on the inner surface with white hairs longer and more abundant near the base; petals lanceolate, acuminate, a third longer than the sepals; staminodia linear-lanceolate, acuminate; style hoary tomentose at the base. Fruit ellipsoidal, covered with rusty brown tomentum, 8–9 mm. long and 5–6 mm. in diameter.

A small tree with slender branchlets thickly covered during their first season with close pale pubescence, and pale and puberulous or glabrous in their second year. Winter-buds ovate, obtusely pointed, thickly covered with pale pubescence, 4–5 mm. long. On vigorous terminal branchlets the pubescence is thicker and light rusty brown.

TEXAS.—Columbia, Brazos County, *B. F. Bush*, October 18, 1900 (no. 1570), September 25, 1901 (no. 914); Houston, Harris County, *E. J. Palmer*, September 17, 1915 (no. 8578), April 29, 1916 (nos. 9608, 9610); Larissa, Cherokee County, June 3 and September 22, 1915 (nos. 7845, 8620); on Spring Creek,

near Boerne, Kendall County, *E. J. Palmer*, April 7 and September 29, 1917 (nos. 11485, 12899); along the southwest bank of the Guadalupe River on the rocky talus in a canyon at the foot of a limestone bluff at Kerrville, Kerr County, *E. J. Palmer*, October 2, 1916 (nos. 10887, 10888 type for fruit), April 8 and June 9, 1917 (nos. 11495, 11501, 11502, 12212, 12213 type for flowers, 12214).

I have not seen leaves and pedunculate bracts with lateral lobes on any other American linden.

TILIA TEXANA var. **grosseserrata,** n. var.—Differing from the type in the coarse serration of the leaves, in the absence of lateral lobes on the leaves and on the bracts of the peduncles, and in the constantly pale, never rusty pubescence of the branchlets and winter-buds.

A small tree with several stems 7–9 m. high, the bark dark gray and rough near the ground and smooth and pale above, in rocky soil at the foot of a limestone bluff by a small stream forming the head of the Sabinal River, near Utopia, Uvalde County, Texas, *E. J. Palmer*, June 17, 1916 (no. 10227 type), April 10 and October 6, 1917 (nos. 11522, 12937).

At the end of their first winter the branchlets of this tree are pale pubescent, puberulous or nearly glabrous, and the winter-buds are reddish or pale brown and glabrous. This linden is interesting as the most western representative of the genus in the United States.

11. **Tilia phanera,** n. sp.—Leaves semiorbicular to broadly ovate, deeply and usually symmetrically cordate at base, abruptly short-pointed at apex, finely dentate with straight or incurved apiculate teeth; when they unfold glabrous above with the exception of a few hairs on the midribs and veins, and thickly coated below with hoary tomentum, and at maturity thin, blue-green, smooth and lustrous on the upper surface, paler and often brownish and coated with a floccose easily detached pubescence of fascicled hairs on the lower surface, 5–9 cm. wide and usually rather broader than long, with slender midribs and primary veins pubescent on the lower surface, and small axillary clusters of rusty brown hairs; petioles slender, coated when they first appear with hoary tomentum, glabrous or slightly pubescent in the autumn, 2.5–4 cm. in length. Flowers 5–6 mm. long, on tomentose pedicels in compact, villose, mostly 16–20-flowered corymbs; peduncle villose, the free portion 1.2–1.5 cm. in length, the bract longer than the peduncle,

short-stalked, obovate, cuneate at base, broad and rounded at apex, floccose pubescent on the lower surface, nearly glabrous on the upper surface; sepals acuminate, pale pubescent on the outer surface, villose along the margins and furnished at the base on the inner surface with a tuft of long white hairs, broader and shorter than the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, style glabrous except at the base. Fruit ellipsoidal, covered with rusty tomentum, 8–10 mm. long and 6–7 mm. wide, on stout, densely floccose-pubescent pedicels.

A tree with slender, light gray-brown, often zigzag branchlets covered when they first appear with fascicled hairs, deciduous during their first summer. Winter-buds ovate, obtusely pointed, terete, reddish brown, glabrous, 4–5 mm. long. Flowers the middle of June. Fruit ripens the end of September.

Banks of Spring Creek, near Boerne, Kendall County, Texas, *E. J. Palmer*, September 27, 1916 (no. 10825 type); April 7 and 11 and June 13, 1917 (nos. 11486, 11593, 12242).

TILIA PHANERA var. **scabrida,** n. var.—*Tilia pubescens* var. a *Aitonii* f. *gymnophylla* V. Engler, Monog. Tilia 130 (in part). 1909. —Differing from the type in the scabrate lower surface of the leaves. Leaves broadly ovate, cordate at base, abruptly short-pointed at apex; when they unfold pubescent above with scattered straight white hairs and hoary tomentose below, and at maturity thin, yellow-green and glabrous above and roughened below by the persistent bases of fascicled hairs, 10 cm. long and broad; petioles 2–2.5 cm. in length. Flowers not collected. Fruit on tomentose pedicels, ovoid to subglobose, covered with pale reddish tomentum.

A small tree with dark deeply ridged bark and glabrous branchlets.

On a low limestone bluff of the Blanco River, near Blanco, Blanco County, Texas, *J. Reverchon*, July 1885 (no. 1500 type), *E. J. Palmer*, April 16 and September 24, 1917 (nos. 11565, 12858); College Station, Brazos County, Texas, *B. F. Bush*, July 4, 1900 (nos. 1915, 4345); Velasco, Brazoria County, Texas, *E. J. Palmer*, March 21, 1918 (no. 13139).

12. **Tilia lasioclada,** n. sp.—Leaves ovate, abruptly contracted at apex into short acuminate points, oblique and truncate or on weak branchlets, often nearly symmetrical and deeply cordate at base, and finely serrate with straight apiculate teeth; when they unfold covered above with soft caducous hairs, pubescent below, and at

maturity thick, bright green, smooth and lustrous on the upper surface, pale and covered on the lower surface with a thick floccose, easily detached pubescence of fascicled hairs, pale on those of lower leaves and often rufous on those of upper branches, 10–15 cm. long and 8–12 cm. wide, the slender midribs and veins covered below with straight hairs mixed with fascicled hairs, and small conspicuous axillary tufts; petioles covered when they first appear with straight hairs mixed with fascicled hairs, soon glabrous, usually 3–4 cm. in length, those of the leaves of weak branchlets very slender and often 5–6 cm. long. Flowers 5–6 mm. long, on stout villose pedicels, in long-branched, mostly 10–15-flowered corymbs more or less thickly covered with straight white hairs; peduncle covered with long white hairs, the free portion 2.5–3 cm. in length, the bract nearly sessile, rounded and unsymmetrical or acute at base, rounded or acute at apex, the midrib more or less thickly covered on the lower side with straight hairs, otherwise glabrous, 2–5 cm. wide; sepals narrow, acute, pubescent on the outer surface, villose on the inner surface, about one-third as long as the lanceolate acuminate petals; staminodia spathulate, rounded and often lobed at apex, about as long as the sepals; style slightly villose at base. Fruit globose or depressed-globose, covered with rusty tomentum, about 1 cm. in diameter.

A tree sometimes 20 m. high with a trunk 30–60 cm. in diameter, stout branches forming a broad round-topped head, and stout red-brown branchlets sometimes glabrous in early summer and sometimes covered more or less thickly during their first and second seasons with long straight hairs.

South Carolina.—Calhoun Falls, Abbeville County; upland woods, Anderson County, *T. G. Harbison*, May 21, 1918; rich wooded slopes near the Savannah River, three miles below Augusta, *T. G. Harbison*, June 17 and August 23, 1916 (no. 8 type), June 17, 1917 (no. 9); Beach Island, a rich wooded slope rising from the north bank of the Savannah River a few miles below Augusta, *R. C. Berckmans*, June 12, 1914.

Georgia.—Shell Bluff on Savannah River 30 miles below Augusta, Richmond County, *C. S. Sargent*, April 6, 1914; steep rocky bluff at the Locks above Augusta, *T. G. Harbison*, May 13, 1913 (nos. 1162, 1163), May 27 and October 6, 1914 (no. 9), April 6, 1916 (no. 6), August 23, 1916 (nos. 12, 13). Brickyard near the Berckman's Nursery west of Augusta, October 5, 1914 (no. 7), August 23, 1916 (no. 16), June 29, 1917 (no. 16), May 31, 1918 (no. 31), May 30, 1918 (nos. 18, 20, 21 type).

FLORIDA.—River Junction, Gadsden County, *T. G. Harbison*, April 25 and September 21, 1914 (no. 1479), April 19 and June 25, 1917 (nos. 116, 119).

From all other American lindens this species differs in the straight hairs on the lower side of the midribs and veins of the leaves, on the peduncle and branches of the inflorescence and on the branchlets, and similar to those of the European *Tilia platyphyllos* Scopoli. The number of these hairs varies on different individuals, and on some trees the branchlets become nearly glabrous by the middle of June, while on others the hairs are present for 2 or 3 years. They are longer and more abundant on the trees growing on the Savannah River at the Locks above Augusta than on trees from other localities, and do not entirely disappear until their third season.

13. TILIA HETEROPHYLLA Ventenat.—Different plants have been referred to this species and it is still by no means clear what should be taken as the type. VENTENAT gives the locality for his tree as "la basse Caroline" where it was discovered by MICHAUX and FRASER. "Basse Caroline" may mean the coast region or the whole state east of the mountains. There is no *Tilia* in the South Carolina coast region which at all agrees with VENTENAT'S description and figure, but near Augusta and in Columbia County, Georgia, and in the neighborhood of Walhalla in Oconee County, South Carolina, on the eastern foothills of the Blue Ridge, a linden is common which in the shape of the leaves agrees better with those figured by VENTENAT than any I have seen. MICHAUX in his journeys from Charleston to the high Carolina mountains went up the valley of the Savannah River and passed by Augusta and through Oconee County, South Carolina. VENTENAT describes the leaves of *T. heterophylla* as snow white on the lower surface. On the Georgia and Walhalla trees the tomentum on the lower surface of some of the leaves is white and on others, especially from upper branches, it is rusty brown, a peculiarity of this tree which is common in other parts of the country. VENTENAT describes the fruit of his tree as globose and 5-ribbed. The fruit which he figured, however, is ellipsoidal and shows no trace of ribs. If the Walhalla trees, as I believe, are to be considered typical of *T. heterophylla* Ventenat, that species may be described as follows:

TILIA HETEROPHYLLA Ventenat, An. Hist. Nat. 2:63. 1800; Mém. Inst. Paris 4:16. *t.* 5.—Leaves ovate, obliquely truncate or rarely slightly cordate at base, gradually narrowed and acuminate

at apex, finely dentate with apiculate gland-tipped teeth; when they unfold pubescent on the upper surface with caducous fascicled hairs, and at maturity dark green and glabrous on the upper surface, covered below with thick, firmly attached, white or on upper branches often brownish tomentum, and usually furnished with small axillary tufts of rusty brown hairs, 8–13 cm. long and 6–10 cm. wide; petioles slender, glabrous, 3.5–4 cm. in length. Flowers 6–7 mm. long on pedicels pubescent with fascicled hairs, in wide mostly 10–20-flowered pubescent corymbs; peduncle glabrous, the free portion 2–4 cm. in length, the bract narrowed and rounded at apex, unsymmetrically cuneate at base, pubescent on the upper, tomentose on the lower surface when it first appears, becoming glabrous, nearly sessile or raised on a stalk up to 1 cm. in length; sepals acuminate, pale-pubescent on the outer surface, villose on the inner surface and furnished at base with a tuft of long white hairs; petals lanceolate, acuminate, a third longer than the sepals; staminodia oblong-ovate, acute, sometimes notched at apex; style villose at base with long white hairs. Fruit ellipsoidal, apiculate at apex, covered with rusty brown tomentum, 7–10 mm. long.

A large tree, with slender, glabrous, reddish or yellowish brown branchlets and oblong-ovate, slightly flattened, glabrous winter-buds 5–7 mm. in length, the outer scales slightly ciliate at apex.

North Carolina.—Falls of the Yadkin River, Stanley County, *J. K. Small*, August 1892; near Newbern, Craven County, *T. G. Harbison*, June 5, 1918 (nos. 42, 44 with styles villose to the middle).

South Carolina.—Walhalla, Oconee County, *T. G. Harbison*, June 4 and 22, 1915, March and October 11, 1917; Russell, Oconee County, *T. G. Harbison*, May 5 and June 29, 1917 (nos. 3, 4), July 7, 1917 (nos. 18, 20).

Georgia.—Cornelia, Habersham County, *T. G. Harbison*, July 7, 1917 (nos. 18, 20); Toccoa, Stevens County, *T. G. Harbison*, June 15, 1918 (no. 9); banks of Flint River, Albany, Dougherty County, *J. K. Small*, May 24–28, 1896, *T. G. Harbison*, June 25, 1915 (no. 3); near Zluguenin, Sumter County, *R. M. Harper*, July 11, 1901 (no. 1049); banks of Savannah River, Germain's Island, Columbia County, *R. M. Harper*, June 1, 1902 (no. 1302).

Florida.—Tallahassee, Leon County, *T. G. Harbison*, June and September 1915 (nos. 1–6); River Junction, Gadsden County, June 1915 and 1916 (nos. 1, 8, 14, 17, 18, 19, 20, 22, 23, 28, 30, 34, 36, 37, 38, 62); Rock Cave, Jackson County, *R. M. Harper*, April 28, 1910; near Marianna, Jackson County, *T. G. Harbison*, September 18, 1916 (nos. 2, 4), May 26, 1917 (no. 21).

ALABAMA.—Berlin, Dallas County, *R. S. Cocks*, June 4, 15, 1915 (nos. 780, 782), July 20, 26, 1916 (nos. 962, 970, 1012), June 18, July 25, 1918 (nos. 790, 792); near Selma, Dallas County, *T. G. Harbison*, April 20, 1915 (no. 22).

WEST VIRGINIA.—White Sulphur Springs, Greenbrier County, *Kenneth Mackensie*, no. 7532 in Herb. Mo. Bot. Gard. (*T. heterophylla* var. *microdonta* V. Engler, Monog. *Tilia*, 135).

INDIANA.—Near Vevay, Switzerland County, *C. C. Deam*, July 25, 1913, June 19 and September 8, 1915 (nos. 13808, 16159, 18806); near the Ohio River, Jefferson County, September 8, 1915 (no. 16219).

On the Florida trees the clusters of hairs at the base of the inner surface of the sepals and the hairs at the base of the style are sometimes wanting; and the fruit is subglobose, sometimes longer than broad or a little broader than long. Like the trees at Walhalla, the tomentum on the under surface of the leaves of the upper branches is usually rusty brown and silvery white on those of the lower branches.

This linden is the common species in the neighborhood of Tallahassee and River Junction, and it appears to have been usually confounded in recent years with a tree of the higher Appalachian Mountains to which I have given the name of *T. monticola*. In the size and shape of the leaves this mountain tree resembles those of *T. heterophylla*, but the tomentum on the lower surface is thicker and whiter and never brown; the petioles are longer and the flowers are nearly twice as large; the branches are red, not yellowish brown, and the winter-buds are larger, more compressed, and bright red.

TILIA HETEROPHYLLA, var. **Michauxii,** n. var.—*Tilia alba* Michaux f. Hist. Arb. Am. **3**:315, *t. 2* (not Linnaeus). 1813; *Tilia heterophylla* Nuttall, Silva **1**:90, *t. 23*. 1842, and of many authors insomuch as relates to the Northern States; *Tilia Michauxii* Nuttall, Silva **1**:92. 1842; Britton and Shafer, North Am. Trees 688 (in part). 1908; Britton and Brown, Ill. Fl. ed. 2, **2**:513 (in part), *fig. 2846*. 1913; *Tilia eburnea* Ashe, BOT. GAZ. **33**:230. 1902; *Tilia apposita* Ashe, Bull. Charleston Mus. **13**:27. 1917; *Tilia tenera* Ashe, *l.c.* 1917.—Differing from the type in the usually cordate, rarely obliquely truncate, more coarsely serrate leaves, broader and more abruptly acuminate at apex, and always white or grayish white, not brownish, tomentose below.

This is one of the most widely distributed of the American lindens, ranging from the valley of the Susquehanna River in Pennsylvania, where it was first noticed by the younger MICHAUX in Lancaster County, to southern and western New York, through southern Ohio and Indiana to northeastern Missouri (Ilasco, Ralls County, *John Davis*, September 30, 1914 (no. 3164), southwestern Missouri (Eagle Rock, Barry County, *E. J. Palmer*, July 16, 1914, no. 6287),

and northwestern Arkansas (Eureka Springs, Carroll County, *E. J. Palmer*, September 21, 1913, no. 4412, Cotter, Marion County, September 1, 1915, no. 8405). Southward it ranges through eastern Kentucky and Tennessee to northeastern Mississippi, along the Appalachian Mountains and their foothills to northern Georgia and to southern Georgia and Dallas County, Alabama. I have not seen specimens of this linden from Illinois, although it may be expected to occur in ravines near the Ohio River in the southern part of the state.

TILIA HETEROPHYLLA var. **nivea,** n. var.—Differing from the type in the whiter tomentum on the lower surface of the leaves, the glabrous styles, in the tomentum on the lower side of the bract of the peduncle at the time the flowers open, the slightly pubescent gray or pale reddish brown branches, and in the puberulous winter-buds.

FLORIDA.—In deep woods, River Junction, Gadsden County, *T. G. Harbison*, April 19 and June 25, 1917 (no. 29 type), June 7, 1915, and June 25, 1917 (no. 27), *A. H. Curtiss*, June 4 and September 13, 1897 (no. 5875).

TILIA HETEROPHYLLA var. **amphiloba,** n. var.—Differing from the type in the fascicled hairs on the upper surface of the young leaves and in the often pubescent branchlets. Leaves broadly ovate, sometimes broader than long, abruptly short-pointed or gradually narrowed and acuminate, or occasionally rounded at apex, symmetrically or obliquely cordate or obliquely truncate at base, finely serrate with apiculate teeth; when they unfold hoary tomentose below and covered above with fascicled hairs, and at maturity thin, dark yellow-green, smooth and lustrous on the upper surface, pale green or brownish and covered below with thick, white, somewhat loose tomentum, on lateral branchlets 4–6 cm. long and 5–7 cm. wide, and on leading shoots 9–10 cm. long and 7–8 cm. wide, the midrib and primary veins covered below with fascicled hairs; axillary hairs rusty brown in small inconspicuous tufts, often wanting; petioles slender, sparingly pubescent when they first appear, becoming glabrous, 2–2.5 cm. in length. Flowers 4–5 mm. long, on stout tomentose pedicels, in broad, thin-branched, slightly pubescent, 7–25-flowered corymbs; peduncle slender, pubescent, the free portion 3–5 cm. in length, the bract oblong to oblong-obovate, cuneate at base, rounded at apex, short-stalked

or nearly sessile, 7 mm.–2.5 cm. in width, thickly covered when it first appears with hoary tomentum, and at maturity tomentose on the upper and pubescent on the lower surface; sepals acuminate, densely pubescent on the outer surface, villose near the margins on the inner surface, about as long as the lanceolate acuminate petals; staminodia oblong-obovate, rounded at apex, about as long as the sepals; style slightly villose at base. Fruit ellipsoidal, covered with rusty brown tomentum, 7–8 mm. long and 5–6 mm. in diameter.

A tree 20 m. high with slender red-brown or orange-brown branchlets glabrous or sometimes covered early in their first season with fascicled hairs. Winter-buds terete, glabrous or when first formed sparingly villose, 2–3 mm. in length. Flowers at the end of June and at River Junction later than the other species with which it is associated. Fruit ripens the middle of September.

FLORIDA.—In woods in sandy soil, River Junction, Gadsden County, *T. G. Harbison*, April 26 and September 21, 1914, April 19 and June 25, 1917 (no. 1484 type), September 21, 1914 (no. 1), June 7 and 28 and September 14, 1915 (nos. 12, 13, 34, 34a, 36, 36a).

ALABAMA.—Valley Head, Dekalb County, *T. G. Harbison*, June 26, 1918 (nos. 42, 42).

I once believed that these trees could be specifically separated from *T. heterophylla*, but their close connection with that species is shown by a tree of *T. heterophylla* var. *Michauxii* which was growing near Tiptop, Tazewell County, Virginia, in May 1914 (*T. G. Harbison*, no. 1616). The upper surface of the leaves of this tree were then covered with fascicled hairs and the branchlets were glabrous. When I visited Tiptop in September of the same year this tree had been cut down, but had produced shoots from the stump which were thickly covered with fascicled hairs and bore large leaves densely pubescent on the upper surface.

14. **Tilia monticola,** n. sp.—*Tilia heterophylla*, Sargent, Silva N. Am., 1:59 (in part, not Ventenat). *t. 27.* 1891; Man. 674 (in part). *fig. 550;* Robinson in Gray Syn. Fl. 1[1]:344 (in part). 1908; Small, Fl. S. States 761 (in part). 1903; Robinson and Fernald, Gray's Man. ed. 7, 566 (in part). 1908; Britton and Shafer, N. Am. Trees 686 (in part). 1908; Britton and Brown, Ill. Fl. ed. 2, 2:512 (in part). 1913.—Leaves thin, ovate to oblong-ovate, very oblique and truncate or obliquely cordate at base, gradually narrowed and acuminate at apex, finely serrate with straight or incurved apiculate teeth, smooth, dark green and lustrous on the upper surface, thickly

coated on the lower surface with hoary tomentum, 10–17 cm. long and 8–12 cm. wide; petioles slender, glabrous, 4–7 cm. in length. Flowers 10–12 mm. long, on stout sparingly pubescent pedicels in mostly 7–10-flowered, thin-branched, glabrous corymbs; peduncle slender, glabrous, the free portion 3.5–4 cm. in length, the bract gradually narrowed and cuneate or rounded at base, narrowed and rounded at apex, glabrous, 10–14 cm. long and 2–2.5 cm. wide, its stalk varying in length from 1 to 2.5 mm.; sepals ovate, acute, ciliate on the margins, covered on the outer surface with short pale pubescence and with silky white hairs on the inner surface; petals lanceolate, acuminate, twice longer than the sepals; staminodia oblong-lanceolate, rounded at the narrowed apex, as long or nearly as long as the petals; style clothed at the base with long white hairs. Fruit ovate to ellipsoidal, covered with pale rusty tomentum, 7–8 mm. long and 6–7 mm. in diameter.

A tree rarely exceeding 20 m. in height with a trunk 1–1.10 m. in diameter, slender branches forming a narrow rather pyramidal head, and stout glabrous branchlets usually bright red during their first year, becoming brown in their second season. Winter-buds compressed, ovate, acute or rounded at apex, light red, covered with a glaucous bloom, 7–10 mm. long. Bark of the trunk 1.5 cm. in thickness, deeply furrowed, the surface broken into small, thin, light brown scales. Flowers from July 12 to July 25. Fruit ripens in September.

NORTH CAROLINA.—Highlands, Macon County, at an altitude of about 600 m., *T. G. Harbison* (many specimens), June, July, and September 1915; Busbee Mountain, near Biltmore, July 5 and September 16, 1897 (ex herb. Biltmore 1030 B).

TENNESSEE.—Johnson City, Washington County, *Gray*, *Sargent*, *Redfield*, and *Canby*, June 21, 1877.

VIRGINIA.—Farmer Mountain, on New River, Cornell County, *J. K. Small*, July 12, 1892, "altitude 2200 feet."

This tree has long been confounded with *T. heterophylla* and its variety *Michauxii*. From these trees it differs in its larger leaves generally more oblique at base, covered below with a denser, always silvery white, tomentum, its longer petioles, its fewer flowered corymbs and in its larger flowers which are larger than those of the other American lindens. It differs, too, in its stouter branchlets, and in the winter-buds which are red, compressed, and much larger than those of other American lindens. At Highlands, North Carolina, where this and *T. heterophylla* var. *Michauxii* are common at altitudes between 400 and 600 m., *T. monticola* flowers 10 or 12 days later than the other tree. The specimen from Johnson City, Tennessee, although it is from a much lower

altitude than the others, is typical of the species, with leaves very oblique at base and up to 17 cm. long on the flowering branches; the petioles vary from 6 to 8 cm. in length. The pedunculate bract is 1.5 cm. in length. At this low altitude the trees naturally bloom earlier than at Highlands. *T. monticola*, with its large leaves snowy white on the lower surface and drooping gracefully on their long petioles, and its large flowers, is the showiest of the American lindens.

15. **Tilia georgiana,** n. sp.—*Tilia pubescens* Ventenat, Ann. Hist. Nat. **2**:62. 1800; Mém. Acad. Sci. **4**:10. *t.* 3 (not Aiton). 1802.—Leaves ovate, slightly unsymmetrical at base and usually cordate on lateral branches and often oblique or truncate on leading branches, abruptly short-pointed at apex, and finely dentate, with glandular teeth pointing forward; when they unfold deeply tinged with red, covered above by fascicled hairs and tomentose below; when the flowers open dark yellow-green, dull and scabrate above and covered below with a thick coat of tomentum, pale on those of the lower branches and tinged with brown on those from the top of the tree, conspicuously reticulate-venulose, and at maturity thick, dull yellow-green, pubescent or glabrous above, rusty or pale tomentose below, sometimes becoming nearly glabrous in the autumn, 6–10 cm. long and 5–8 cm. wide; petioles slender, tomentose, 2–4 cm. in length. Flowers 6–7 mm. long, on slender pubescent pedicels in compact, slender-branched, pubescent, mostly 10–15-flowered corymbs; peduncle slender, pubescent on the lower, nearly glabrous on the upper, surface, the free portion 2.5–3 cm. in length; sepals ovate, acuminate, coated on the outer surface with pale pubescence and on the inner surface with pale hairs longest and most abundant at the base, not more than one-half the length of the lanceolate acuminate, narrow petals; staminodia oblong-obovate to spathulate, acute, about two-thirds as long as the petals; style glabrous or furnished with a few hairs at the very base. Fruit on pubescent pedicels, depressed-globose, occasionally slightly grooved and ridged, covered with thick rusty tomentum; 5–6 mm. in diameter.

A tree with slender branchlets thickly coated during their first season with pale tomentum, and dark red-brown or brown and puberulous in their second year. Winter-buds covered with rusty brown pubescence, 6–7 mm. long. Flowers the middle of June. Fruit ripens early in September.

South Carolina.—Near Charleston, *T. G. Harbison*, September 4, 1916 (no. 16).

Georgia.—Colonel's Island, near Dunham, Liberty County, *T. G. Harbison*, September 9, 1916 (nos. 4, 5, 8, 9), June 19, 1917 (no. 19); Brunswick, Glynn County, *T. G. Harbison*, May 24, June 19, September 2 and 3, 1916 (nos. 6, 7 type, 10, 11, 13, 15).

Florida.—San Mateo, Putnam County, *A. H. Curtiss* (no. 401a), Gainsville, Alachua County, *T. G. Harbison*, June 10 and September 10, 1915, June 21 and September 14 and 15, 1916, April 24 and 25 and June 15, 1917; Lake City, Columbia County, *G. V. Nash*, July 11–19, 1895, *T. G. Harbison*, June 14, 1915, September 16, 1916, April 22 and June 23, 1917; Sumner, Levy County, *T. G. Harbison*, June 12, 1915, September 12, 1916, April 25, June 15 and September 25, 1917; Tallahassee, Leon County, *T. G. Harbison*, April 14, 1916; Crawfordville, Wakulla County, *R. M. Harper*, June 19, 1914 (no. 211); Marianna, Jackson County, *T. G. Harbison*, September 19, 1916 (no. 8), April 20 and May 26, 1917.

What is perhaps best considered a variety of this species may be described as—

Tilia georgiana var. **crinita**, n. var.—*Tilia pubescens* Sargent, Silva N. Am. 155, *t. 26* (in so far as relates to South Carolina, not Aiton); Man. 675. *fig. 55.* 1905.—Differing from the type in the longer and more matted, usually rusty brown hairs of the pubescence, usually less closely attached to the under surface of the leaves and often very conspicuous on the young branchlets.

South Carolina.—Sandy woods, Bluffton, Beaufort County, *J. H. Mellichamp*, May 28, 1887; near Charleston, *T. G. Harbison*, September 6, 1915 (no. 13).

Georgia.—Colonel's Island, near Dunham, Liberty County, Miss *Julia King*, July 1915, *T. G. Harbison*, September 8, 1916 (nos. 1, 2).

This linden has a general resemblance to *T. Houghii* Rose, which differs in its rather looser pubescence and large and conspicuous tufts of hairs in the axils of the veins. Moreover, it hardly seems possible that a tree known only at a few stations on the coast of South Carolina and Georgia should also grow south of the City of Mexico, and so far as is now known nowhere else.

Arnold Arboretum
Jamaica Plain, Mass.

THE PURPLE HYACINTH BEAN

GEORGE F. FREEMAN

(WITH SEVEN FIGURES)

Students of the genus *Dolichos* are now somewhat perplexed concerning the identity of *D. lignosus* Linn. and *D. Lablab* Linn. According to accepted usage, the former name applies to the small-leaved perennial vine sparingly grown as a greenhouse climber in northern climates and for arbors and trellises in warmer countries. CURTIS (Bot. Mag. 1797, p. 380) states that it is perennial in England. *D. Lablab* is generally understood to refer to the common hyacinth bean or Bonavist, which has large purple leaves and racemes of showy purple flowers and seeds which are mottled mahogany brown to black. There are a number of varieties of this species, some of which have white flowers, white seeds, and green leaves. The size of the seed and the length and compactness of the racemes also vary strongly in the different kinds. This plant is strictly annual in the United States. It is used as an ornamental climber for porches, summerhouses, etc.

Now PRAIN (Jour. Asiatic Soc. Bengal **66**[2]:429–430. 1897) reverses the incidence of these names and makes *D. Lablab* refer to the perennial species and *D. lignosus* to the annual hyacinth bean.

In the 1895 edition of *Index Kewensis*, JACKSON does not recognize *Dolichos lignosus* as a valid species, but makes *D. lignosus* Jacq. Select. Am. 205 equal *D. Jacquini* DC. Prod. **2**:397, Ind. occ.; and he makes *D. lignosus* Linn. Sp. Pl. 726 equal *D. Lablab* Linn. Sp. Pl. 725, Reg. trop. Again, PIPER (U.S. Dept. Agric. Bull. 318. 1915. p. 5), evidently following PRAIN and JACKSON, accepts the validity of *D. Jacquini* DC. Prod. **2**:397 and assigns to this species the small perennial variety of *Dolichos* formerly grown in various parts of the world as *D. lignosus* Linn.

These references to LINNAEUS are to the edition of 1753, which is now the recognized beginning date of the binomial nomenclature. Evidently LINNAEUS considered these two species as distinct. If

we are to follow the *Index Kewensis* in this matter we must assume that LINNAEUS was mistaken and that he had only two divergent forms out of the many varieties into which we now know *D. Lablab* to be subdivided. The evidence available, however, does not support this view, but indicates rather that the plants from which these two species were described were really specifically distinct. The original descriptions from *Species Plantarum* (pp. 725, 726) are as follows:

1. DOLICHOS leguminibus ovato-acinaciformibus, seminibus ovatis. *Lablab* hilo arcuato versus alteram extremitatem. *Roy. lugdb.* 368. *Hort. ups.* 214.
Phaseolus aegyptius, nigro semine, *Bauh. pin.* 341.
Phaseolus niger Lablab. *Alp. aegypt.* 74. t. 75. *Vest. aegypt.* 27.
Habitat in Aegypto.
Legumina *dorso scabra.* Caules ramique *teretes, retrorsum scabri.* Pedunculi *semiverticillati.*

9. DOLICHOS caule perenni, pedunculis capitatis, leguminibus *lignosus* strictis linearibus.
Dolichos caule perenni lignoso. *Hort. cliff.* 360. t. 20.
Phaseolus indicus perennis, floribus purpurascentibus. *Eichr. carol.* 36.
Habitat . . . .

Of the identity of *D. Lablab* L. we have no doubt. The original description corresponds exactly with the plant grown today under the name hyacinth bean. This is further confirmed by the presence in the herbarium of the Linnean Society of London of a specimen of this plant identified and written up by LINNAEUS himself. In fig. 1 is given a tracing of this specimen which was very kindly furnished by the general secretary of the Linnean Society.[1] The identity of this plant with the common hyacinth bean is evident. Compare fig. 2, which is a photograph of a specimen grown by the writer. The references given by LINNAEUS to "Bauh. pin. 341" and "Alp. Aegypt. 74 t. 75" have been examined and leave no doubt but that they refer to the common hyacinth bean. The reference to "Roy lugdb. 368, Hort. ups. 214" has not been available.

[1] This tracing was kindly obtained for the writer by Dr. OAKES AMES of Harvard University.

The confusion has evidently arisen on account of the uncertainty as to the identity of the plant described by LINNAEUS as *D. lignosus*. There is no cut accompanying this description, but LINNAEUS refers to an earlier publication by himself (Hort. Cliff.

FIG. 1.—Tracing of specimen of *Dolichos Lablab* identified and described by LINNAEUS; from specimen in herb. Linnean Society.

360. t. 20) and to "Eichr. Carol. 36." This latter publication has not been available, but the former has been examined carefully. Fig. 3 is a reproduction of a photostat copy of LINNAEUS' figure in Hort. Cliff. 360 t. 20. The description accompanying this plate was much more full and complete than that in the *Species Plantarum* of 1753, and moreover was evidently made from a

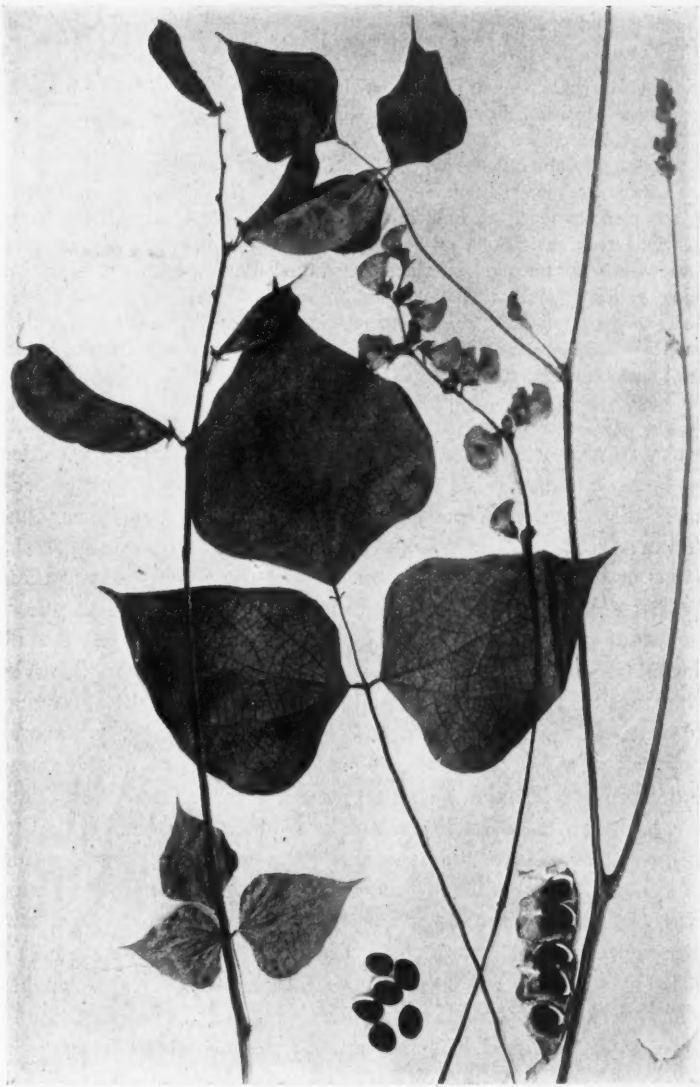

FIG. 2.—Purple hyacinth bean (*Dolichos Lablab*): photograph of specimen grown at University of Arizona, 1914.

fresh specimen before him. This description may be quoted as follows:

2. Dolichos caule perenni lignoso. Vide Tab.
Phaseolus indicus perennis, floribus purpurascentibus. Hort. Carolsrb. 36.
Crescit in America.

Ante accessum nostrum enata fuit planta frutescens arcte scandens, plus quam homanae altitudinis; caule tereti, contorto, vix striato, ramis plurimis tenuibus. Folia ad ramorum exortum ternata, petiolo communi insidentia, quorum quod intermedium ovato-cordatum, acuminatum, latitudine pollicis, glabrum, petiolo proprio quaduplo reliquorum productiori insidens; lateralia latere exteriori magis dilatata, interiori vero dimidio angustiora. Flores in pedunculo pauci, corolla rubra seu purpurea. Absoluta florescentia absque fructu periit.

It should be noted in this description that although the plant was 6 ft. or more, the leaves were but 1 inch wide and are recorded as being smooth. This plant, which was probably the only specimen of *D. lignosus* actually seen by LINNAEUS, bloomed freely but did not set seed. LINNAEUS therefore probably never saw the seeds or pods of this species, but quoted the descriptions of these organs in his later publications from descriptions by other authors of plants which he assumed to be of the same species. Here in all probability lies the source of confusion. LINNAEUS had observed that his *D. Lablab* was an annual in Europe and did not know that in warmer countries this same species may persist as an herbaceous perennial. When therefore he met with a *Dolichos* which was described as perennial, he would naturally be inclined to associate it with a species of *Dolichos* which he knew to be perennial, that is, his own *D. lignosus*. Thus he made the error in the 1763 edition of *Species Plantarum* (p. 1022) of citing *Phaseolus perennis* of Rümph. Amb. 5, pp. 378 t. 136, as a synonym of his *D. lignosus*, although this species (which is clearly *D. Lablab*) is described by RÜMPHIUS, in the publication named, as having leaves 3–4 inches long and nearly as broad, with racemes 1 ft. long and bearing many flowers. RÜMPHIUS' plate, a reproduction of which is given in fig. 4, could scarcely be assumed to represent the same plant as that of *D. lignosus* in Hort. Cliff. 360. The only point of similarity is in

FIG. 3.—*Dolichos lignosus* Linn.: from photostat copy of LINNAEUS' figure in *Hortus Cliffortianus*.

the flower clusters, and here the descriptions show these to be entirely distinct (see legend to fig. 4).

Turning to the descriptions and plates left by other botanists of the immediately succeeding decades we find in JACQUIN *Selectarum stirpium Americanarum historia* (1763) a plant described as *D. lignosus*. Citations to the *D. lignosus* of Linn. Sp. Pl. 726 and Linn. Hort. Cliff. 360. t. 20 are given with question marks, indicating that the author doubted that the plant he described was the same as that described by LINNAEUS. An examination of his description makes it clear that the two plants were entirely different, for the plant of JACQUIN had pilose stems and pods, peduncles shorter than the scabrous leaves, white flowers, and pods 3–4 inches long, containing about 18 seeds, whereas, as we shall see, the plant described by LINNAEUS had nearly smooth stems, pods, and leaves, peduncles longer than the leaves, purple flowers, pods 1–2 inches long with 7 or 8 seeds at the most.

AITON (Hort. Kew. 3:31, 33. 1789) recognizes both *D. Lablab* L. and *D. lignosus* L. and gives practically the same descriptions as are given by LINNAEUS. He states that *D. lignosus* was introduced into England in 1776 by MONF. THOUIN.

In 1792 SMITH (Spicilegium Bot. no. 2, Gleanings of Botany, pp. 19 and pl. 21) describes and pictures a plant which he calls *D. lignosus*. SMITH'S plate is here reproduced in fig. 5 and his description is so clear and concise that it is quoted in full as follows:

TABLE XXI

Dolichos lignosus. Purple woody Dolichos. Diadelphia Decandria. Stigma downy.

GEN. CHAR. Standard marked at its base with two parallel oblong tubercles, compressing the under side of the wings.

Section 1. Climbers

SPEC. CHAR. Stem climbing, perennial. Flowers in little heads. Pods straight, linear.

Syn. *Dolichos lignosus* Linn. Sp. Pl. 1022. Hort. Cliff. t. 20. Ait. Hort. Kew. V. 3.33.

A native of the East Indies.

Root woody, perennial. Stem woody, supple, climbing, much branched, roundish, striated, smooth; branches alternate, very long and slender, but

FIG. 4.—*Phaseolus perennis* Rümph. Amb. 5. 378. t. 136: the description accompanying this plate states that the racemes are 1 ft. long and many-flowered; plant here represented is undoubtedly *D. Lablab* Linn.

little subdivided, round, striated, somewhat downy, leafy, many-flowered. Leaves alternate, on long footstalks, ternate, or rather binate with an odd one.

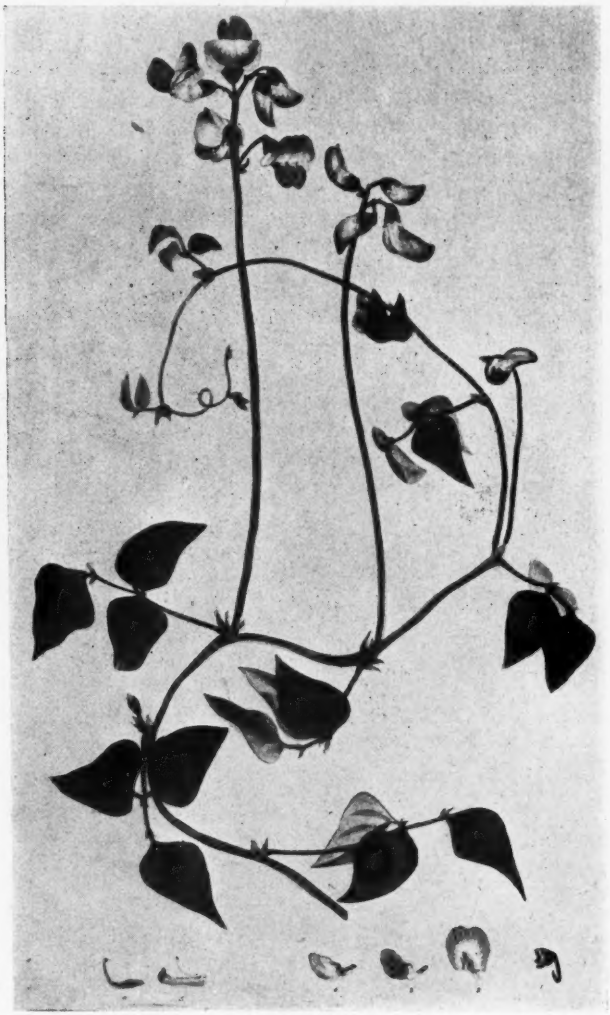

FIG. 5.—*Dolichos lignosus:* reproduction of pl. 21, J. E. SMITH, Spicilegium Bot. no. 2. Gleanings of Botany. 1792.

Common footstalk roundish, channeled above, swelling and purplish at the base; partial ones very short, swelled, incurved. Leaflets rhomboid, elongated, acute, entire, obsoletely 3-nerved; bright green and shining above; glaucous beneath. Stipulae entire, sharp, somewhat triangular, downy on the margin, dark purple at the base; of which 2 larger ones are placed at the bottom of the common footstalks, and 2 smaller, lanceolate, at the insertion of the partial footstalks. Clusters axillary, solitary, erect, each having from 3 to 6 flowers in a little head. Common flowerstalk simple, very long, striated, angular in the upper part; partial ones generally 2 together, short, downy, single-flowered.

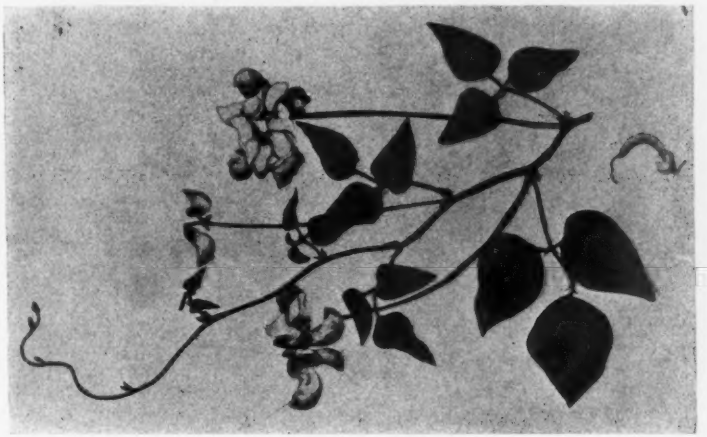

FIG. 6.—*Dolichos lignosus:* from photograph of colored plate in CURTIS' Bot. Mag. 2:380. 1797.

Bracteae lanceolate, acute, hairy. Flowers somewhat drooping, rose coloured with a purplish keel. Calyx smooth, thickly ciliated in the margin. Pod an inch long, a little recurved, brownish, smooth. Seeds black.

According to AITON, this beautiful plant was introduced from the French gardens to our own in 1776. It is easily propagated by seed, and in a stove produces abundance of flowers during the summer.

A little study of SMITH's plate and descriptions shows that it agrees very closely with the plate and description of *D. lignosus* of LINNAEUS and that it cannot possibly be the *D. lignosus* of JACQUIN.

Five years later, in CURTIS' Bot. Mag. 11:380. 1797, is found a description and plate of *D. lignosus*, which is reproduced in fig. 6.

Comparing the plate and description with those of SMITH and LINNAEUS, there is no doubt that they all had the same plant. Finally, fig. 7 is made from a fresh specimen of plants grown at the University of California. This plant agrees perfectly with SMITH'S description and with every essential part of the description and

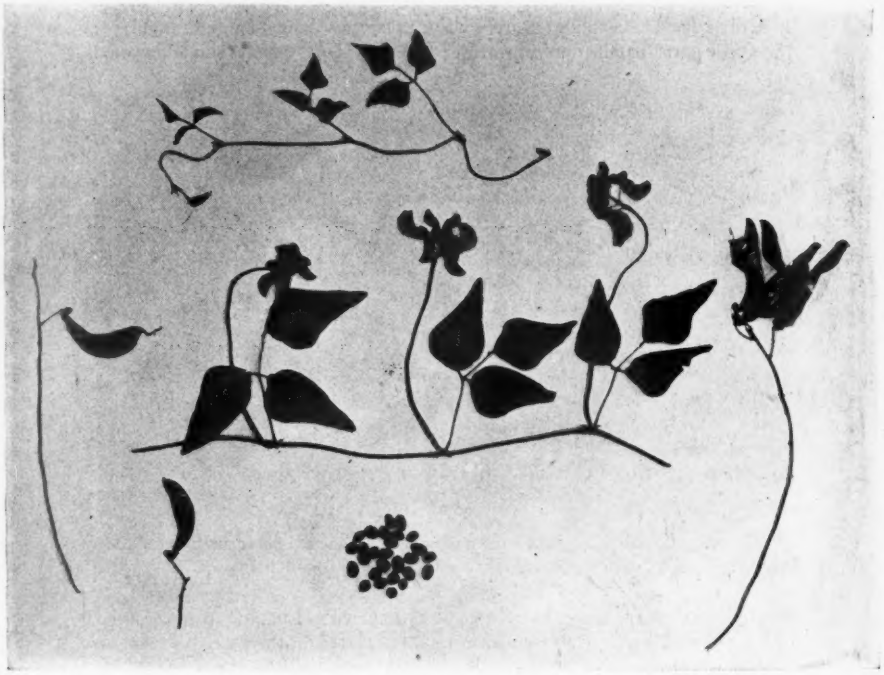

FIG. 7.—*Dolichos lignosus:* from photograph of fresh specimen furnished by Professor GREGG, University of California, January 1914.

plate by LINNAEUS except that in which he states that the pods are straight. When we remember that LINNAEUS probably never saw the pods of this species, such a discrepancy is not surprising.

Misled by the error of LINNAEUS in ascribing straight pods to his *D. lignosus*, DECANDOLLE (Prod. 2:397. 1825) makes the *D. lignosus* of CURTIS (Bot. Mag. t. 382[2]) a variety of *D. lignosus* Linn. He moreover corrects the error made by JACQUIN in assign-

[2] This is an error by DECANDOLLE, and should read 380.

ing his plant (described in Select. Stirp. Amer. Hist. 1763, p. 205) to *D. lignosus* L. by calling this plant *D. Jacquini*. To emphasize the justice of this disposition of the 2 species by DECANDOLLE, the original description furnished by JACQUIN may be quoted as follows:

> Planta perennis, volubilis, tota pilosa; praecipue vero rami inferiores lignosi, and legumina, pilis hispida sunt. Foliola sunt ovata, acuta, scabriuscula, duos pollices longa, lateralibus interne obliteratis. Stipulae ex lanceolato ovatae, acuminatae, basi emarginatae. Pedunculi umbellati, foliis breviores, pauciflori. Flores albidi. Legumina tres quatuorve pollices longa, acuminata, stricta, ad apicem leviter incurva, teretia, nec torosa, pilossissima fusca, interne nivea. Semina circiter octodecem, nitida, atra cum hilo albido, parva, compressiuscula, ex oblongo reniformia.
>
> Habitat in Caribaearum sylvaticis.

It would be difficult to harmonize this description with that of either SMITH (Spic. Bot. no. 2, p. 19) or LINNAEUS (Hort. Cliff. 360. t. 20). We must conclude, therefore, with DECANDOLLE, that it is a distinct species and follow him in calling it *D. Jacquini* DC. Prod. 2:397.

In the opinion of the writer, the evidence presented herewith is sufficient to show that the plants described as *D. lignosus* by LINNAEUS (Sp. Plant. ed. 1, 1753, p. 726), and more fully in his earlier work (Hort. Cliff. 360. t. 20. 1737), by J. E. SMITH (Spic. Bot. no. 2, p. 19, pl. 21. 1792), by CURTIS (Bot. Mag. 11:380. 1797), and the plant now grown in various parts of the world as *D. lignosus* and shown in fig. 7 are all one and the same species, which is distinct from *D. Lablab* L. We are therefore unable to follow either JACKSON (Index Kewensis 1895) in making *D. lignosus* L. a synonym of *D. Lablab* L; PRAIN (Jour. Asiatic Soc. Bengal 66²:429–430. 1897) in reversing the incidence of the original Linnaean names by making *D. Lablab* L. refer to the perennial species and *D. lignosus* L. to the annual hyacinth bean; or PIPER (U.S. Dept. Bull. Agr. 318. 1915, p. 5), in assigning the plant commonly grown as *D. lignosus* L. to *D. Jacquini* DC. On the other hand, we must hold to the original Linnaean designation of the common annual (frequently perennial in tropical countries) hyacinth bean (and its many varieties, fig. 2) as *D. Lablab* L., and the more slender perennial greenhouse (in northern climates) climber shown in fig. 7 as *D. lignosus* L.

AGRICULTURAL EXPERIMENT STATION
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A MORPHOLOGICAL STUDY OF PALLAVICINIA LYELLII

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 245

ARTHUR W. HAUPT

(WITH PLATES XX–XXIV)

Pallavicinia, according to SCHIFFNER'S (12) census, is represented by 21 species, most of which are tropical. Later, SCHIFFNER (13) added 2 European species to his former list, thus making 5 species indigenous to the Old World. *Pallavicinia Lyellii* is found in the more humid parts of both the Northern and Southern Hemispheres; it grows near Chicago in a peat bog at Mineral Springs, Indiana. *Pallavicinia*, *Symphyogyna*, and *Monoclea* are included in the family Leptotheceae. The affinities of the Japanese genus *Makinoa*, described by MIYAKE (9), seem to place it in this family, as is done by CAVERS. The disposition of *Monoclea* is a matter of great difference of opinion, some, as JOHNSON (6), placing it with the Marchantiales. There can be no doubt, however, as to the closeness of relationship between *Pallavicinia* and *Symphyogyna*, regardless of the classification of the other genera of the family.

CAVERS (2) divides *Pallavicinia* into the two genera of GOTTSCHE: *Blyttia* and *Mörckia*. According to the Vienna code, the older name *Pallavicinia* must be retained; if SCHIFFNER'S subgenus *Mörckia* (Gott.) is to be elevated to generic rank, it must not be done at the expense of the name *Pallavicinia*. STEPHANI (14) separates the genus into the 2 sections PROCUMBENTES and DENDROIDEAE; SCHIMPER, into the subgenera *Eupallavicinia*, *Mörckia*, and *Mittenia*. *Pallavicinia Lyellii* belongs to the PROCUMBENTES or *Eupallavicinia* division.

Material

Most of the material studied was collected by Mr. R. P. MASON, at Columbiana, Alabama, to whom the writer is greatly indebted. Additional material was obtained by Dr. W. J. G. LAND, at Mineral Springs, Indiana. Most of the slides illustrating the antheridial

series were made by Dr. LAND and Mr. MASON, while those showing the development of the archegonium and the sporophyte were prepared by the writer.

Thallus

The vegetative body of *Pallavicinia Lyellii* consists of a creeping, prostrate thallus 4–5 mm. wide, composed of a midrib with thin, one-layered, lateral wings, and bearing rhizoids. The margin is somewhat undulate, with no indications of hooked appendages as in *P. longispina*, *P. xiphioides*, or *P. Zollengeri*. The midrib consists of pitted conducting cells with thickened walls, which become differentiated directly behind the apical cell (fig. 45); about 70 to 80 may be seen in cross-section (fig. 44). TANSLEY and CHICK (**15**) made a careful study of these cells and showed by eosin solutions that they conduct water. Miss MCCORMICK (**8**) demonstrated that in *Symphyogyna aspera* they are composed of pectose. These conducting cells are also found in *Hymenophyton*.

Growth of the thallus is by means of a dolabrate (zweischneidig) apical cell (fig. 43). This feature seems to have first been observed by LEITGEB (**7**), who discusses at considerable length apical growth and the development of the thallus body. Two-celled mucilage hairs arise both dorsally and ventrally in connection with the apical cell, strongly resembling sex organ initials.

Branching is of two kinds: apical, from the apical cell; and endogenous, from ventral adventitious shoots. Material showing the origin of the latter was lacking and hence LEITGEB'S statement, that the conducting tissue of the ventral branch is not continuous in origin with the central cells of the main thallus, could not be verified.

Sex organs

The gametophytes of *Pallavicinia Lyellii* are strictly dioecious, the male plants being slightly more slender than the female. Both antheridia and archegonia are dorsal, the former lying in 2 parallel rows on each side of the midrib, and the latter remaining directly above the midrib, slightly raised on a pad. Two involucres are present, the outer one corresponding to that of *Symphyogyna* and *Monoclea;* the inner one, or perianth, is characteristic of *Pallavicinia*, *Podomitrium*, and *Calycularia*.

ANTHERIDIA

The antheridia originate in close proximity to the apical cell, arising in acropetal succession on the dorsal side of the thallus, usually singly, but occasionally two or three together. With further apical divisions they come to lie in 2 parallel rows on each side of the midrib, slightly sunken in the thallus by the development, from behind, of an involucral upgrowth. The mature antheridia are spherical and short-stalked and point diagonally outward and upward, each one being separated from the one preceding it by sterile tissue (fig. 1).

An antheridium initial appears as a papillate projection above the surface of the thallus, resembling closely one of the mucilage hairs with which it is associated. A transverse wall appears, dividing the initial into 2 nearly equal segments, the basal one remaining in the thallus and the outer one projecting above the surface of the thallus (fig. 2). The outer cell divides transversely into equal segments, forming a primary stalk cell and a primary antheridial cell (fig. 3). With further increase in size, the latter divides by a median vertical wall, followed rapidly by a similar division in the stalk cell (fig. 4). One or two further transverse divisions complete the stalk, while a periclinal wall cuts off a peripheral cell on one side of the antheridium, intersecting the first vertical wall near the top (fig. 5). A corresponding periclinal wall appears on the other side, followed by 2 more walls at right angles to the first two, intersecting both these and the first median division. As a result, 4 primary wall cells inclose 2 central cells, the entire structure being bisected by the original vertical wall. At this stage the involucre appears as an upgrowth of the thallus behind the young antheridium (fig. 9). It is built up by basal growth, and by the time the antheridium is mature, it consists of a scalelike sheath, 6–10 cells in length. Whether these coverings are to be regarded as the beginnings of true foliar structures or merely as dorsal upgrowths of the thallus seems to be entirely a matter of opinion. If the complete involucre of *Pellia* be taken as representing the initial stage, a failure of the forward portion to develop would result in the precise condition found in *Pallavicinia*. *Sphaerocarpus*, perhaps, represents an intermediate stage, as here the development of

the forward portion is slightly arrested, resulting in greater protection from behind. It seems a perfectly logical step from the antheridial condition in *Pallavicinia* to that of one of the simpler acrogynous Jungermanniales, such as *Porella*, in which case the coverings are longer and more leaflike in appearance.

Further growth of the antheridium corresponds to that of the other anacrogynous Jungermanniales. During the 2 or 3 mitoses preceding the formation of the sperm mother cells, the cell walls of the spermatogenous mass gradually disappear and abundant mucilage surrounds the dividing protoplasts. Walls around the sperm mother cells were evident, but it could not be determined whether they had been laid down by the mother cell protoplasts, or represented the remaining cellulose which had not become mucilage. The sperm mother cells produce two sperms, each with little cytoplasm, and separated by a very thin wall. The nuclei were so small that it was not possible to study the details of spermatogenesis. The development is probably the same as that of *Pallavicinia Zollengeri*, described by CAMPBELL and WILLIAMS (1).

ARCHEGONIA

The earliest stages in the development of the archegonial group were not present in the material studied. A group of initials seems to arise a short distance back of the apical cell, directly above the midrib on the dorsal side of the thallus. This group presently becomes surrounded by an annular upgrowth of the thallus, which becomes the involucre. The apical cell is not checked by the development of the archegonia, but continues the growth of the thallus, so that often 2 or 3 groups may be produced along the midrib, separated by sterile areas. The archegonial group continues to produce archegonia up to the time of fertilization, many young sex organs frequently being found with mature ones. Two-celled mucilage hairs are abundantly produced. Twenty to 30 archegonia usually occur in a group.

The archegonium, like the antheridium, arises as a papillate projection from one of the cells inclosed by the involucre. A transverse wall cuts off a basal cell, which remains within the thallus, and an outer cell, which is freely exposed (fig. 10). The latter

undergoes 2 transverse divisions, the sequence of which could not be determined; the lower 2 cells form the stalk and the upper one the archegonium proper, agreeing in this repsect with *Pallavicinia radiculosa*, described by CAMPBELL and WILLIAMS (figs. 11, 12). Three vertical divisions occur in the archegonium proper, according to the manner of all anacrogynous Jungermanniales, resulting in the formation of an inner cell surrounded by 3 primary wall cells, 2 of which can be seen in a longitudinal section (fig. 12). A transverse division in the upper part of the inner cell results in the formation of a central cell and a cap cell (fig. 13), which later undergoes further division, contributing to the development of the neck.

Following the formation of the cap cell, the central cell divides into two nearly equal cells (fig. 14), the upper being the primary neck canal cell, and the lower the primary ventral cell. The development of the axial row usually precedes the division of the primary ventral cell, although frequently mitoses can be seen in the neck cells after the formation of the ventral canal cell and egg (fig. 22). In most cases about 10 neck canal cells were seen; sometimes, however, as many as 18 are formed (fig. 25). The primary ventral cell, by a transverse division, produces a ventral canal cell and egg which are almost equal in size (fig. 18). The neck canal cells are surrounded by a jacket of 5 cells, although frequently one or more of these may divide (fig. 24).

Very soon after the division of the ventral cell the ventral canal cell becomes mucilaginous and finally the entire axial row is broken down (figs. 19, 20). The egg nucleus at this stage is very prominent, the dense nucleolus being surrounded by extremely light nucleoplasm. With the preparation of the egg for fertilization, the wall of the venter becomes 2-layered, the first divisions occurring as the ventral canal cell begins to disorganize. The mature archegonium is characterized by a rather long slender stalk, a narrow venter, and a long twisted neck; it closely resembles an archegonium of *Symphyogyna*.

Just before the older archegonia in a group mature the characteristic perianth appears immediately within the involucre. It attains a height of several cells (fig. 21), but as soon as fertilization is effected, it is greatly stimulated, and develops, by basal inter-

calary divisions, much in excess of the young sporophyte. The perianth keeps pace with the elongation of the embryo, reaching a maximum height of about 5 mm. At the time immediately preceding spore disperal, the seta shows remarkable growth, becoming 25–27 mm. long. The perianth attains a thickness of 3 or 4 cells, as seen in cross-section, and becomes fringed around the top. The involucre, on the other hand, does not at any time exceed the height of the archegonia and it is related to their protection in the same way that the perianth is associated with the protection of the sporophyte. With the development of the perianth, following fertilization, the involucre becomes flaring and denticulate around the top.

After fertilization the egg cytoplasm becomes denser and a heavy wall is laid down around the protoplast, thus making it independent of the tissue of the archegonium.

Sporophyte

The youngest sporophyte which was observed consisted of a tier of 4 cells (fig. 26). The first division is followed by a transverse wall in the lower segment and then by a similar wall in the upper segment. A vertical division then occurs in the upper half of the embryo (figs. 27, 28), followed by vertical and transverse walls. The lower half of the embryo usually undergoes one vertical division, but contributes nothing to the development of the foot, seta, or capsule (fig. 29). Half of the potentially sporogenous tissue derived from the fertilized egg thus is diverted for haustorial purposes. A similar situation has been observed by Miss CLAPP (3) in *Aneura pinguis*, and by CAMPBELL and WILLIAMS in *Pallavicinia Zollengeri*. The relation between the early divisions in the embryo and the development of the 3 regions of the sporophyte could not be ascertained, material being wanting. The differentiation of the sporogenous tissue, however, occurs relatively late. According to FARMER (4), the young embryo of *Pallavicinia decipiens* consists of a tier of 3 cells, the upper segment forming the capsule, the middle segment the seta and part of the foot, and the lower segment the rest of the foot.

With the growth of the embryo, the venter of the archegonium becomes a calyptra 4 or 5 cells in thickness, which grows in length

with the sporophyte. The calyptra is notably smaller than in *Symphyogyna* and *Monoclea*, presumably because its protective function is performed by the perianth. The non-functioning archegonia are carried up with the tissue of the calyptra but do not persist long. Only one embryo was seen developing in an archegonial group, although it is possible that more than one may be formed, as in *Symphyogyna aspera*.

The differentiation of the spores and elaters occurs late in the development of the sporophyte, and follows precisely the method of *Symphyogyna aspera*, as described by Miss McCORMICK (figs. 33–38). Material showing the reduction division in the formation of spores was entirely absent in the material studied. FARMER (5), in his study of this process in *Pellia epiphylla* and *Pallavicinia decipiens*, noted the presence of a quadripolar spindle in the spore mother cell. MOORE (10, 11), however, working with *Pallavicinia Lyellii*, failed to find such a condition, but observed that the two divisions take place in very rapid sequence, giving the appearance of such a spindle as FARMER describes.

The mature capsule is cylindrical, is inclosed by a sterile wall one cell thick, and bears spiral thickenings (figs. 32, 39). The sterile cap at the apex of the mature capsule is not so prominent as in *Symphyogyna*, being only 5 or 6 cells thick, and bears no relation to the elaters. The mature sporophyte reaches a length of 40 mm., the capsule being about 3.5 mm. long. Dehiscence is by means of 4 longitudinal slits which remain attached at the top. The foot is wedge-shaped as in *Symphyogyna*, but it occasionally shows a resemblance to the anchor-like foot of *Marchantia* (figs. 41, 42). The mature elaters reach a length of nearly 0.3 mm., and are furnished with a double spiral band. The spores are about 0.015 mm. in diameter, the wall being conspicuously reticulate (fig. 38).

Summary

1. *Pallavicinia Lyellii* belongs to the subgenus *Eupallavicinia*, the vegetative body consisting of a single prostrate portion.

2. The apical cell is of the dolabrate type. Branching is both apical and adventitious.

3. *Pallavicinia Lyellii*, like the other species of the genus, is strictly dioecious.

4. The antheridia occur in 2 parallel rows on each side of the midrib, and are protected from behind by an involucral upgrowth. Their development, with minor variations, follows the type for the anacrogynous Jungermanniales.

5. The archegonia are in dorsal groups and are surrounded by an involucre and a perianth, the latter remaining inconspicuous until after fertilization.

6. The young archegonial stalk consists of 2 cells. The egg is small and the neck long and twisted.

7. The lower half of the fertilized egg becomes a haustorial organ and contributes nothing to the development of the foot, seta, or capsule.

8. The calyptra is 4 or 5 cells in thickness, in this respect differing from that of *Symphyogyna*.

9. The differentiation of the spores and elaters occurs relatively late in the development of the sporophyte, and follows the method of *Symphyogyna*.

10. A sterile cap is present at the apex of the capsule and remains intact in dehiscence, which is accomplished by means of 4 longitudinal slits.

To Dr. W. J. G. Land, under whose direction the study was undertaken, the writer is indebted for many helpful suggestions and criticisms.

University of Chicago

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EXPLANATION OF PLATES XX–XXIV

Pallavicinia Lyellii

FIG. 1.—Thallus with antheridia; ×10.

FIGS. 2–7.—Stages in development of antheridium; ×630.

FIG. 8.—Older antheridium; ×62.

FIG. 9.—Young antheridium with involucre; ×46.

FIGS. 10–20.—Stages in development of archegonium; ×520.

FIG. 21.—Perianth before fertilization; ×50.

FIG. 22.—Archegonium showing elongation of neck; ×50.

FIG. 23.—Median longitudinal section of archegonial group; ×25.

FIG. 24.—Cross-section of neck of archegonium; ×520.

FIG. 25.—Mature archegonium showing 18 neck canal cells; ×260.

FIGS. 26–28.—Stages in development of embryo; ×520.

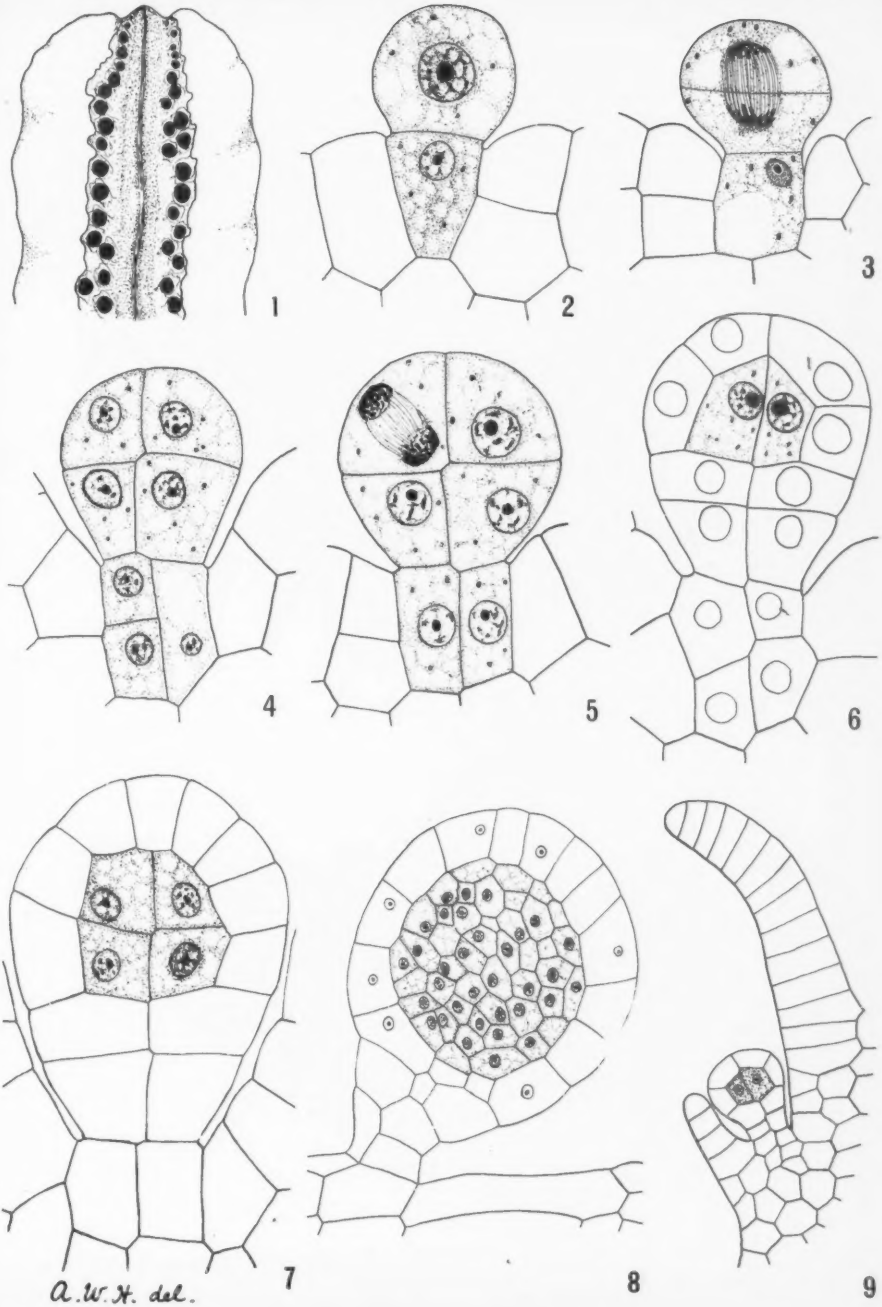
FIG. 29.—Older embryo showing haustorial cells and differentiation of sporogenous tissue; ×50; sketch of same stage; ×8.

FIG. 30.—Development of sporogenous tissue; ×50; sketch of same stage; ×8.

FIC. 31.—Sketch of older sporophyte; ×6.

FIG. 32.—Sporophyte containing mature spores and elaters; ×6.

FIGS. 33–37.—Stages in development of spore mother cells; ×520.



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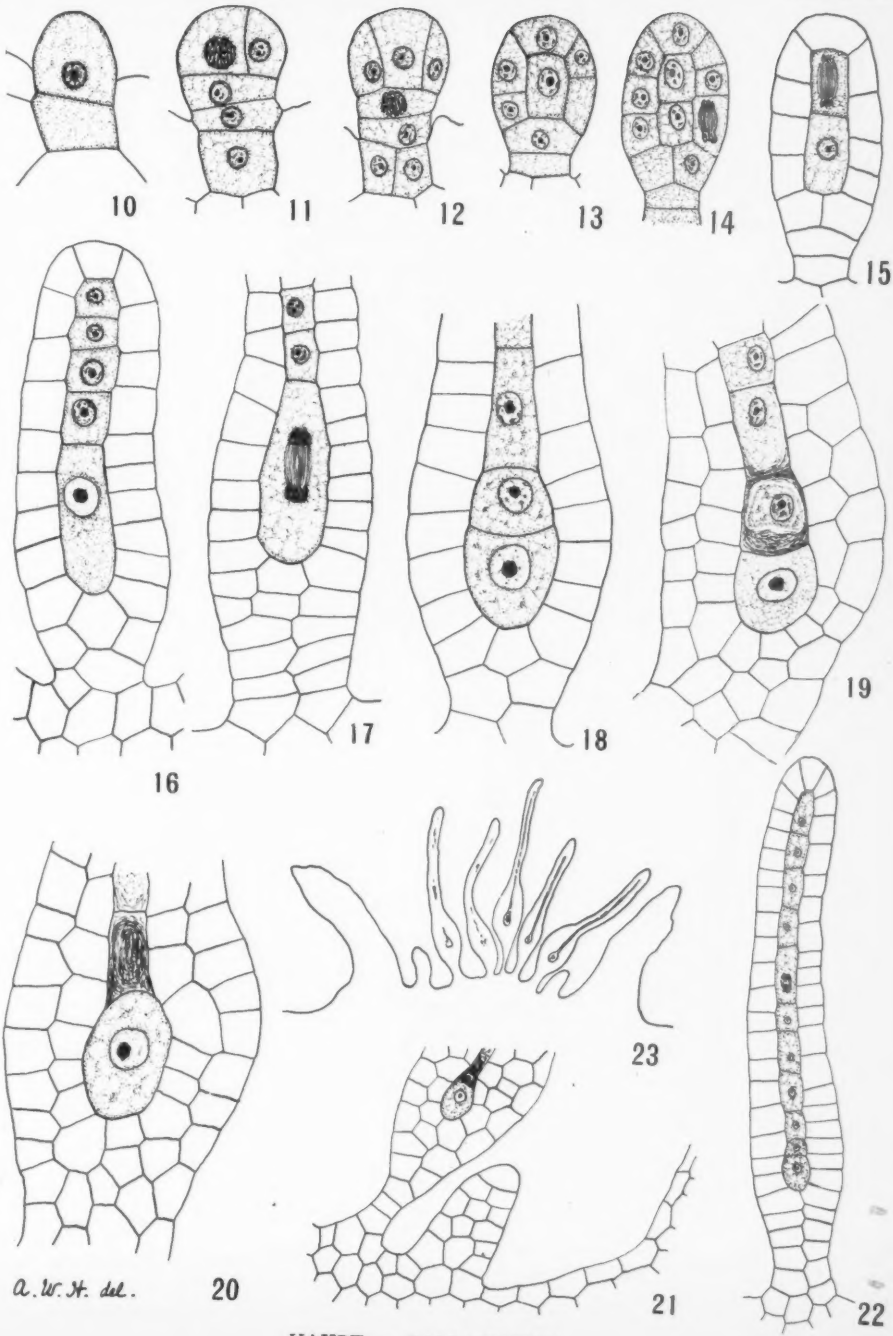

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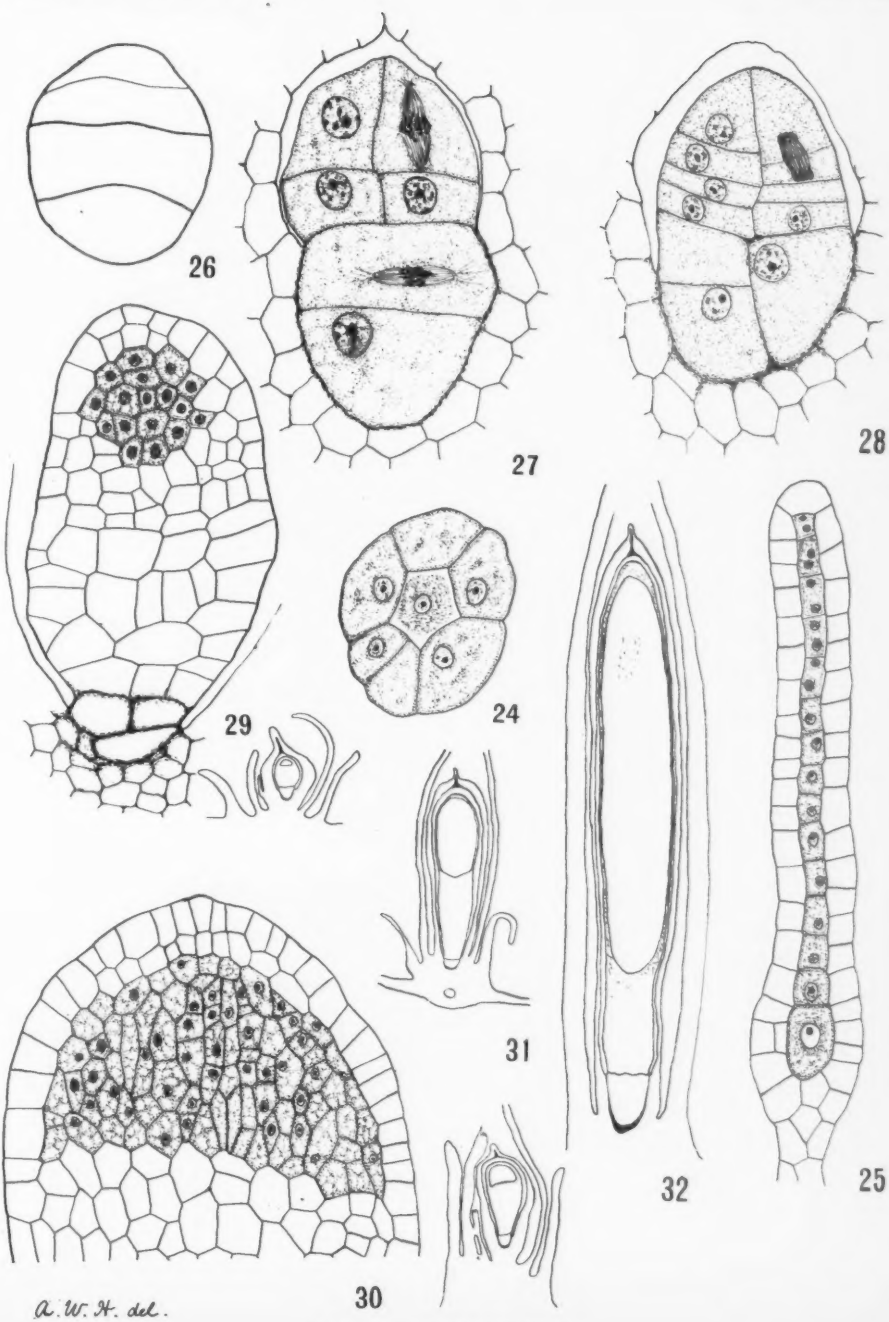

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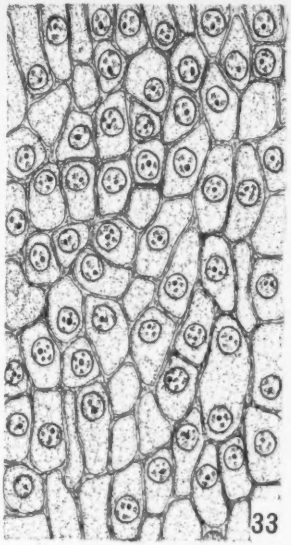
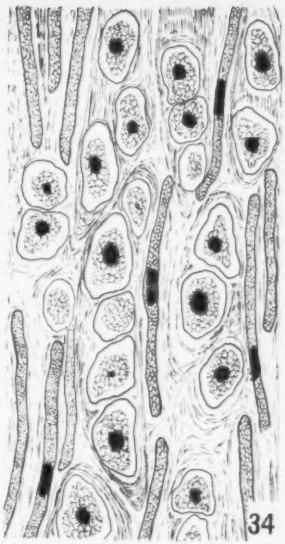
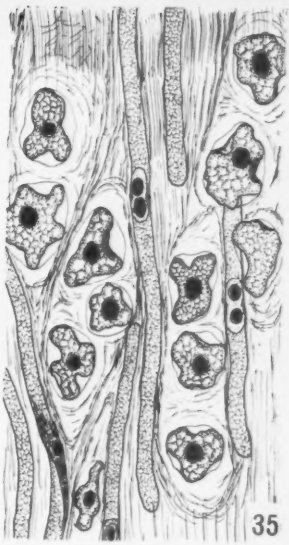
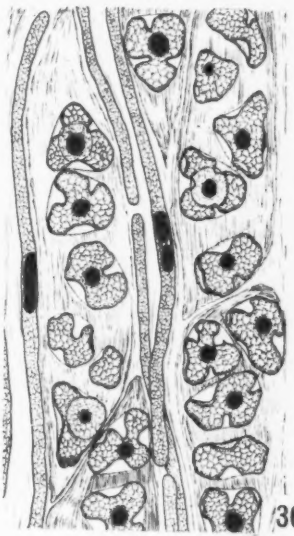
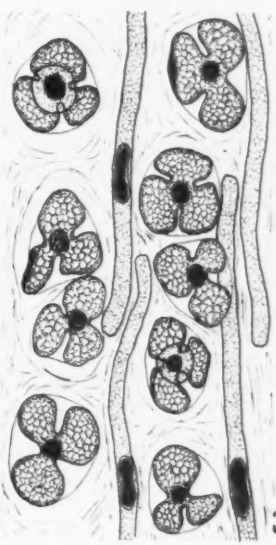
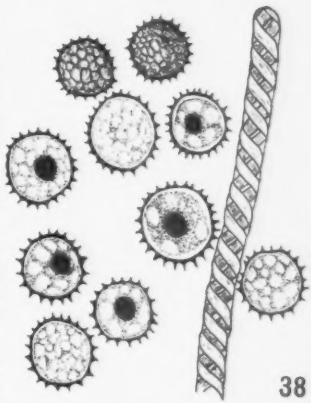


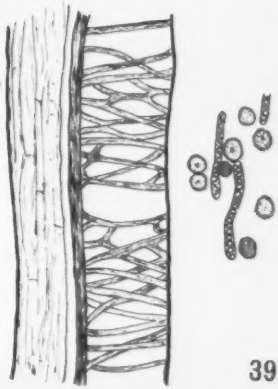


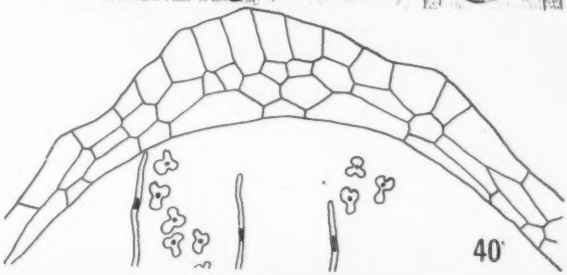




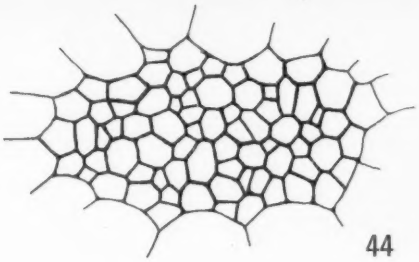








HAUPT on PALLAVICINIA



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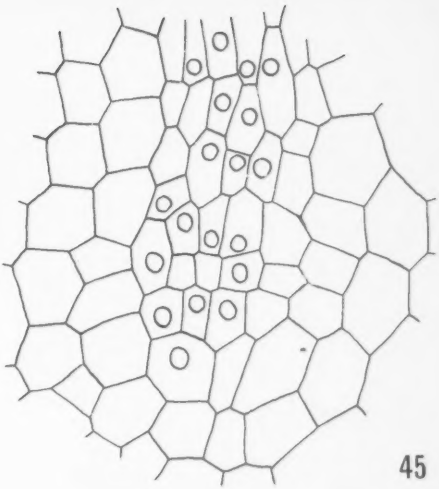

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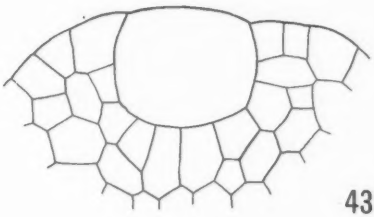

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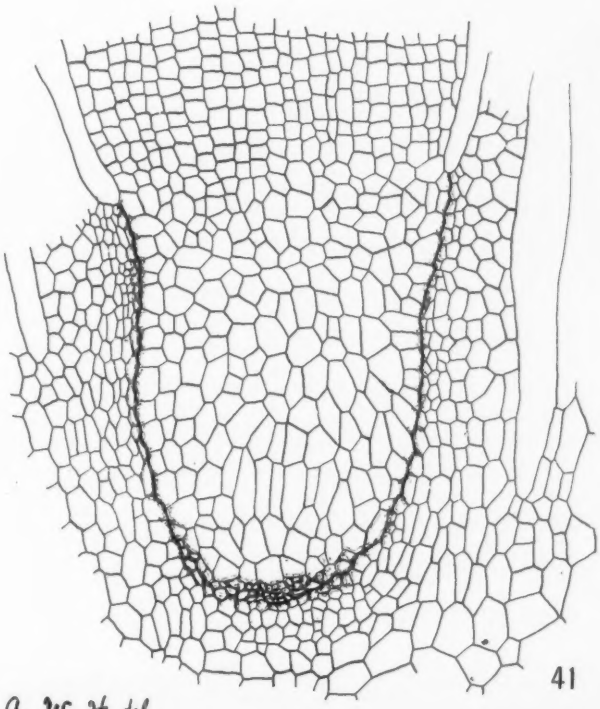

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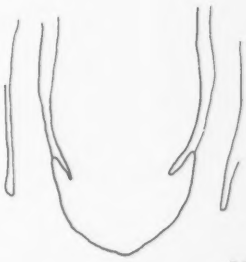

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a. W. H. del.

HAUPT on PALLAVICINIA

FIG. 38.—Mature spores and elater; ×630.

FIG. 39.—Wall of mature capsule and calyptra; ×30.

FIG. 40.—Median longitudinal section of sterile cap of capsule in mother cell stage; ×50.

FIG. 41.—Typical foot of mature sporophyte; ×30.

FIG. 42.—Anchor-like foot of sporophyte; ×15.

FIG. 43.—Median longitudinal section of apical cell; ×50.

FIG. 44.—Cross-section of cells in conducting strand; ×520.

FIG. 45.—Median longitudinal section of region directly back of apical cell showing differentiation of conducting cells; ×520.

FIG. 46.—Conducting cells showing pits; ×520.

FIG. 47.—Part of same; ×1040.

BRIEFER ARTICLES

MODIFICATION OF HAND MICROTOME

(WITH FIVE FIGURES)

Figs. 1–5 represent a simple modification of the familiar hand microtome, and one which has been found to be a decided improvement over the original instrument from which it was derived. In the ordinary type, when cutting sections of woody stems or more delicate material held in pith, it is always difficult to be certain of obtaining the necessary pressure for holding the material at the proper point. The steel rod which moves in or out upon the turning of the single pressure screw will usually hold the material firmly at its lower end but not so firmly at its upper end, with the result that the material has a tendency to wobble when the knife begins to cut the section. On the other hand, when this difficulty does not arise it is often almost impossible to screw up the material for the next section because of the pressure of the material against the walls of the tube or well.

To obviate these rather commonly encountered difficulties in the ordinary type of hand microtome the modification of it shown in the figures was devised. Figs. 4 and 5 give two views of an inner "material holder." It consists of two pieces of curved steel which are long enough to reach to the bottom of the tube or well (just below *cc* in fig. 2). This inner material holder is provided with a spreading spring at *ed* which surrounds a small steel bar *cc*. Each curved piece of steel has a hole at *aa* (fig. 4) through which project the ends of the two pressure screws *bb* (fig. 2). The manipulation of the apparatus is as follows where, for example, cross-sections of a woody stem are to be cut. The pressure screws *bb* are turned out until their ends at *aa* are pulled out of the holes in the material holder. The microtome is inverted and the material holder falls out. The stem or a portion of it is placed between the leaves of the material holder and properly oriented and, if necessary, a rubber band is bound around the material holder just above *aa*. The material holder containing the stem is now pushed down into the well or tube of the microtome and oriented so that the holes are opposite the ends *aa* of the turned-back pressure screws. These screws are

turned in, their ends pass into the holes in the material holder, and pressure is finally exerted on both sides. As the pressure becomes

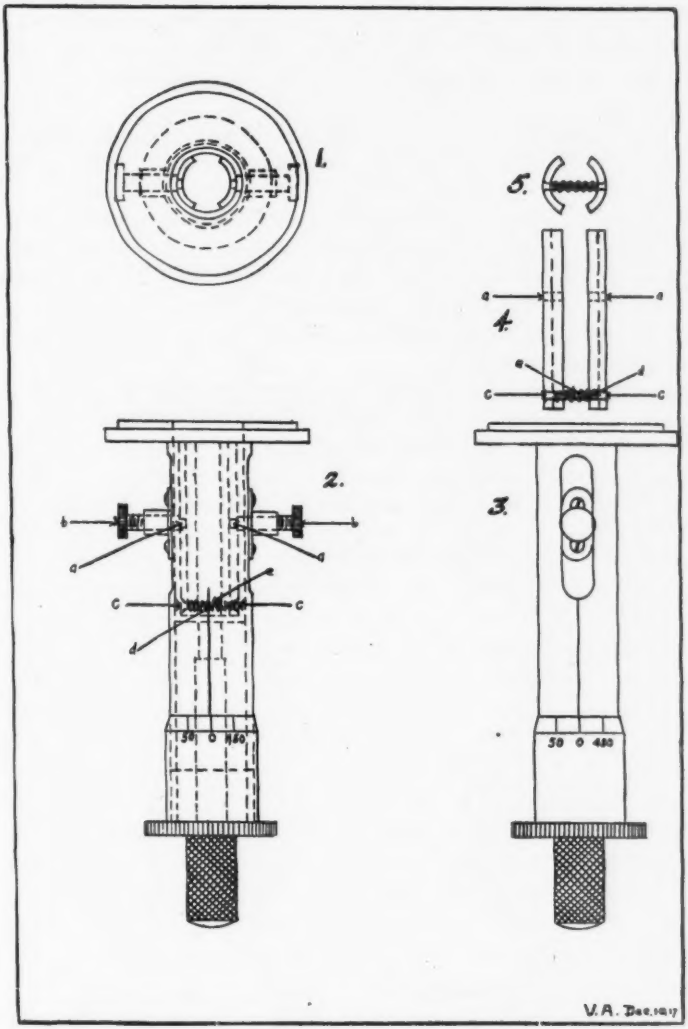

FIG. 1.—Modification of hand microtome

greater, the spring at *de* prevents the upper ends of the material holder from spreading and insures maximum pressure against the material at these upper ends. Finally the stem is held firmly in the center of the tube or well of the microtome between the leaves of the material holder. The pressure screws are free to move up or down in their openings because no appreciable pressure is exerted upon the walls of the tube or well.

In a similar manner material held in pith is very conveniently arranged in this apparatus. The possibility of arranging and orienting such material held in pith in the material holder outside the microtome is an obvious advantage. Longitudinal sections of small woody stems are readily cut in this modified hand microtome, whereas their small diameter makes it very difficult to secure them firmly in the original apparatus. As may be seen, it is possible to orient material to obtain all angles in the case of sections to be cut obliquely or in the case of unsymmetrical material.

This modified hand microtome was devised to meet a special need and has admirably served its original purpose. This description of it is presented primarily because it illustrates the possibility of modifying an apparatus in a relatively simple and inexpensive manner to increase greatly its convenience and the range of its usefulness. The original modification from which the drawing was made has been somewhat improved recently. The knurled heads *bb* should be much larger than those illustrated, and for woody stems the leaves of the material holder should be thicker and their inner surfaces more nearly flat.—T. H. GOODSPEED, *University of California.*

CURRENT LITERATURE

MINOR NOTICES

Fungous diseases and insect pests.—In a small volume issued as one of the Cambridge Farm Institute Series, PETHERBRIDGE[1] gives a popular account of the more common fungous diseases and insect pests of farm crops. The book is designed to be helpful to farmers and others who wish to acquire a knowledge of such things. The treatment is very elementary, but sufficiently extensive to give the uninitiated some idea of the nature of fungi and insects and their relation to agricultural crops. The text is nearly equally apportioned between the two main divisions of the subject-matter. The first division deals with fungi and fungous diseases, and the second with insect pests. Each division is introduced by a general chapter giving in each case a brief description of fungi, their mode of life, and the part they play in crop economy; and in the second part a general account of the structure, life histories, and habits of insects. In the special chapters the plan is followed of describing in detail some of the representative types of fungi and insects, as for instance, *Erysiphe graminis* as an example of the mildews, and grouping around them others of similar nature. An idea of the scope of the work can best be gained from the chapter headings, as follows: Introduction to fungi; Potato diseases and allied diseases; Finger and toe, and wart disease; Mildews; Ergot and clover sickness; Rusts; Smuts; Introduction to insects; Butterflies and moths; Beetles; Flies; Aphids and sawflies; Eelworms.

The book is written in a clear style and it will undoubtedly prove useful to the farmers of England in enabling them to identify the common insect and fungous diseases, and to find means of combating them. In the more extensive and diversified agriculture of the United States, where a vast special literature dealing with each particular condition is already available to the farmer, the book would find little application.—H. HASSELBRING.

Flora of the Northern Territory of Australia.—EWART and DAVIES[2] have published a flora of the large area known as the Northern Territory of Australia, not merely as a contribution to taxonomy, but also as an indication of "the fertility of the soil, the moisture conditions, and the fodder or other values of

[1] PETHERBRIDGE, F. R., Fungoid and insect pests of the farm. Cambridge. 1918.

[2] EWART, ALFRED J., and DAVIES, OLIVE B., The flora of the Northern Territory. 8vo. viii+387. *pls.* 27. Melbourne. 1917.

the natural vegetation." There are lists of plants of fodder value, valuable woods, poisonous and injurious plants, and medicinal plants. Four appendices also deal with Cyperaceae, Myrtaceae (except *Eucalyptus*), *Eucalyptus*, and *Acacia*. Four new genera are established by EWART as follows: *Spathia* and *Setosa* (Gramineae), *Rossittia* (Rutaceae), and *Carpentea* (Convolvulaceae); and in addition 30 new species are described.—J. M. C.

NOTES FOR STUDENTS

Phenomena of parasitism.—In a summary of his researches on the processes involved in the attacks of plant tissues by *Botrytis cinerea*, BROWN[3] gives a review of the work already published and a forecast of investigations now in progress. The published work has already been noted in this journal,[4] and we need only allude to the author's speculation on the question whether the effects produced by the fungous extract on the cell wall and on the protoplasm are attributable to the same or to different substances. In the absence of any means of disentangling the mixture of substances occurring in plant extracts or of excluding the action of all but one, it seems futile to speculate on the specificity of action of any of the substances. Future work as outlined by the author is to cover such problems as the germinating capacity of spores in water and in nutrient solutions, the diffusion of substances from plant cells into water placed on the cuticle, and the physics of cuticular resistance.

The fourth contribution to this series[5] deals with some of the factors influencing the production of cytase in cultures of *Botrytis cinerea*. In the first paper of the series it was shown that very active cytolytic extracts could be obtained from young germ tubes of the spores of the fungus. As might be expected, therefore, the activity of the enzyme extracted from cultures of different ages is proportional to the quantity of actively growing mycelium. Consequently, with respect to enzymatic activity, a growing culture soon reaches a maximum, and thereafter the enzyme content rapidly diminishes. The enzyme content of the culture fluid follows a course in general parallel to that of the mycelium. Dilution of the enzyme extract by a similar extract deactivated by exposure to a temperature of 65° has the same effect as dilution by distilled water. The lower enzyme content of old cultures, therefore, is not caused by the development of inhibiting substances. As might appear self-evident, cultures thickly sown with spores gave stronger enzyme extracts than cultures thinly sown. The experiments confirm the former conclusions that enzyme production is restricted to the growing ends of the hyphae.—H. HASSELBRING.

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[3] BROWN, W., On the physiology of parasitism. New Phytol. **16**:109–126. 1917.

[4] Rev. BOT. GAZ. **61**:80. 1916; **63**:240. 1917.

[5] BROWN, W., Studies in the physiology of parasitism. IV. On the distribution of cytase in cultures of *Botrytis cinerea*. Ann. Botany **31**:489–498. 1917.

Phytogeography of South Africa.—The very diverse vegetational types of South Africa have been classified and mapped by EVANS[6] in such a manner as to give a good idea of the ecological divisions of the southern part of that continent. The woodland has been subdivided into forest, scrub, bushveld, and palmveld. The first of these, which is mostly evergreen, is dominated by species of *Podocarpus*, while the scrub is a type of Sclerophyllous Shrub, in which the Proteaceae, Ericaceae, and Restionaceae contribute the dominant forms. From this the bushveld differs in its deciduous character and also in its more parklike aspect and its floristic composition. Bushveld is widely distributed, and while dominated by *Acacia* spp., such genera as *Tamarix*, *Combretum*, *Ficus*, *Zizyphus*, and *Rhus* are of common occurrence. The palm belt comprises a littoral strip on the southeast in which such palms as *Mimusops caffra*, *Phoenix reclinata*, *Raphia vinifera*, and *Cocos nucifera* mingle with succulents from the genera *Aloe* and *Euphorbia*.

The grassland covers the greater portion of the country with transitions to scrub and desert. That of the Kalahari region occupies much of the central portion of South Africa with an open formation, short, low, wiry grasses, species of *Aristida* and *Eragrostis*, occurring in isolated tufts. This and the other grasslands show transitions to the desert toward the west.

Four distinct desert types are briefly characterized and mapped, perhaps the most remarkable being the southern portion, a vast shallow basin, the Karroo, sparsely populated by succulent, tuberous, and bulbous plants. Prominent genera are *Crassula*, *Mesembryanthemum*, *Cotyledon*, *Euphorbia*, *Aloe*, *Stapelia*, *Senecio*, *Encephalartos*, and *Euclea*.

More important perhaps than the text, at least for the American botanist, are the excellent plates, enabling one to visualize the different types, and the map showing their distribution.—GEO. D. FULLER.

Pigment production in Penicillium.—BRENNER,[7] investigating the production of pigment in cultures of *Penicillium*, finds that in the absence of magnesium in the culture medium, or in the presence of ammonium salts whose utilization leads to an acid reaction of the culture fluid, no red, but only yellow pigment is produced. The red pigment is produced only in neutral media or in media developing an alkaline reaction. Iron apparently is not necessary for the formation of the red color. The author further reports a few preliminary experiments on the extraction and chemical reactions of the pigment which is insoluble in ether, chloroform, toluene, and similar organic solvents, but soluble in alcohol and dilute alkalies or ammonia. On account of the acid nature of the pigment the author attributes to it the physiological function of maintaining the neutrality of the medium.

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[6] EVANS, F. B. POLE, The plant geography of South Africa. Dept. Agric. Union of South Africa. Official Year Book. 1917. pp. 8. *pls. 24. map.* 1918.

[7] BRENNER, W., Die Farbstoffbildung bei *Penicillium purpurogenum*. Svensk. Bot. Tidskr. 12:91–102. 1918.

Many investigations have been made on the so-called influence of various environmental factors on the production of pigments by fungi, but a survey of the facts seems to indicate that between the absorption of an elementary nutrient and the production of a complex pigment two processes intervene to permit of the establishment of a direct relation between stages at the extreme ends of the series. A much better knowledge than is at hand at present of the nature and structure of fungous pigments is necessary before their physiological status can be determined. Different colors may often be due to the modification of the same pigment, depending on different reactions of the medium.—H. HASSELBRING.

Origin and goal of geobotany.—RÜBEL[8] has issued a compact and useful paper, dealing with the main phases of the development of geobotany and with the aims of its various subdivisions. Geobotany he regards as embracing all interrelations between plants and the earth, including much of ecology, chorology, chronology, and genetics; thus it includes all of phytogeography in the widest sense, and more. The historical presentation deals especially with the work of THEOPHRASTUS, TOURNEFORT, LINNAEUS, HALLER, SOULAVIE, WILLDENOW, HUMBOLDT, WAHLENBERG, and SCHOUW. Geobotany may be either floristic or vegetational, each of which subdivisions may consider the problems of space (distribution), habitat (ecology), or change (genetics). Thus RÜBEL recognizes 6 fields of geobotany: autochorology, or floristics; synchorology, or the distribution of plant associations; autecology, or the relation between the individual and the habitat; synecology, or the relation between the plant association and the habitat; autogenetics, or the change of floras; and syngenetics, or the change of plant associations. It appears to the reviewer that this is the most logical classification of these fields of study with which he is familiar. As a matter of practice, however, it is unlikely that investigators will increasingly recognize such subdivisions. A treatise dealing only with synchorology was fairly satisfactory in times gone by, but in these days it would seem sterile, except as livened up with ecology and genetics.—H. C. COWLES.

Continuous variation.—STOUT and BOAS,[9] as the result of their extensive statistical studies of variation in *Cichorium*, recommend that critical study of species variation should be based upon intensive studies of partial (existing among the parts of a single individual) and individual (characteristics of plants as wholes based on their entire record) variabilities. They suggest that failure to appreciate this necessity has allowed considerable error to creep into the work of a number of investigators. For example, hereditary studies of such

[8] RÜBEL, EDUARD, Anfänge und Ziele der Geobotanik. Vierteljahrsschrift der naturforschenden Gesellschaft in Zürich **62**:629–650. 1917.

[9] STOUT, A. B., and BOAS, HELENE M., Statistical studies of flower number per head in *Cichorium Intybus:* kinds of variability, heredity, and effects of selection. Mem. Torr. Bot. Club **17**:334–458. *pls. 10–13.* 1918.

characters as the size of flowers should be prefaced by an accurate knowledge of how such characters vary with relative place position on the plant or relative time position in the total period of bloom.

The authors have been able to isolate and maintain a number of races, but further state that "within each race there are further variations, continuous in gradation and of the same nature as those appearing in a more mixed population, which are unmistakable evidences of the instability of characters and hereditary units."—MERLE C. COULTER.

New-place effect.—COLLINS[10] has performed a rather unusual experiment with maize, testing the immediate effect of transferring various races to new habitats. We have abundant testimony that it is unwise to go very far from home for seed corn, and have generally concluded that local corn has become the best adapted to local conditions as the result mainly of artificial selection, whether conscious or unconscious. In accordance with this we should naturally suppose that to transfer seed would depress its yield (for a few generations at least). COLLINS, however, shows that while Texas seed of a given strain, planted side by side in Maryland with Maryland seed of the same strain, exceeds the latter in yield by 8 per cent; when the two are grown in Texas the Texas seed exceeds in yield the Maryland seed by only 2 per cent. It seems that the transfer of Maryland seed has acted as a stimulus to relatively greater yield. This phenomenon is termed "new-place" effect. It adds a further complication to the already perplexing problem of vigor in maize.—MERLE C. COULTER.

Dominance and parasitism.—JONES[11] finds support of his theory[12] that dominance accounts for hybrid vigor, from observations on susceptibility to parasitism in maize. It has hitherto been demonstrated by several investigators that resistance to parasitism behaves as a definite heritable factor. JONES shows that inbreeding corn serves to isolate certain homozygous races which are susceptible to smut and leaf blight while the more heterozygous ancestors are resistant. He concludes that "as in so many other cases, those factors which enable an organism to attain the best development tend to dominate." Thus, in general, the most heterozygous corn, which therefore shows the greatest hybrid vigor, will be the most resistant. A difficulty arises here, since certain diseases are known to thrive best in the most vigorous plants. It might be possible to account for this difference on the ground that certain diseases are immediately destructive to the host while others are not; although if this were true, JONES's leaf blight disease and smut should behave differently.—MERLE C. COULTER.

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[10] COLLINS, G. N., New-place effect in maize. Jour. Agric. Research **12**:231–243. 1918.

[11] JONES, DONALD F., Segregation of susceptibility to parasitism in maize. Amer. Jour. Bot. **5**:295–300. 1918.

[12] Rev. BOT. GAZ. **66**:70. 1918.

Lichen growth.—As the results of experiments and observations extending over a period of 8 years, FINK[13] has determined the rate of growth in certain crustose and foliose lichens, as determined by measurements of the diameter of the thallus, to vary from increases of 0.36 cm. per year for *Umbilicaria pustulata*, and 0.42 cm. for *Physica pulverulenta*, to 1.3 cm. per year for *Parmelia Borreri* and *P. caperata*, and 1.75 cm. for *Peltigera canina*. Some of the intermediate annual increments were 0.2–0.75 cm. for *Graphis scripta*, 0.6 cm. for *Verrucaria muralis*, and 1.16 cm. for *Parmelia conspersa*. In these measurements FINK has given us practically the only definite data we possess relative to the increase in size of these pioneer plants. With regard to migration, FINK declines to indulge in speculations regarding possible methods, and says "nothing is definitely known further than seeing parts of *Cladonia* thalli lying on some of the quadrats in early stages of ecesis."—GEO. D. FULLER.

Vegetation studies in Natal.—BEWS continues his interesting studies of the vegetation of Natal,[14] his latest paper dealing with the ecology of the Drakensberg.[15] These mountains exhibit picturesque and even stupendous scenery, the highest peaks being more than 11,000 ft. above the sea. The most extensive formation, as elsewhere in Natal, is the veld or grassland. The alpine veld is composed more of tussock grasses than is the lowland veld, and the growth forms are more xerophytic. An interesting formation is the *Protea* veld, dominated by various species of small trees of the genus *Protea*. The climax formation is the bush, dominated by species of *Podocarpus*, and occupying the more protected situations. The mountain top vegetation is markedly xerophytic, and is dominated by composites (as *Helichrysum*) and heathers (as *Erica*). The last section of the paper deals with successions and interrelations.—H. C. COWLES.

Tree growth in Iowa.—In presenting data upon tree growth in the vicinity of Grinnell, Iowa, CONARD[16] brings out several interesting facts in addition to the average annual increment of several species. There seems to be conclusive evidence that trees are encroaching upon the grasslands, and this is ascribed to the elimination of prairie fires during the past half century. While this accounts for the present increase of forested areas, it is not regarded as explaining the presence of grasslands which constituted the natural vegetation upon the best soils in the region. These richer soils are very favorable to tree growth and the increments are sufficiently large to indicate that timber would

[13] FINK, BRUCE, The rate of growth and ecesis in lichens. Mycologia **9**:138–158. 1917.

[14] BOT. GAZ. **64**:85–86. 1917.

[15] BEWS, J. W., The plant ecology of the Drakensberg Range. Annals Natal Museum **3**:511–565. *pls. 4. figs. 3.* 1917.

[16] CONARD, H. S., Tree growth in the vicinity of Grinnell, Iowa. Jour. Forestry **16**:100–106. 1918.

prove a profitable crop. Some typical average annual increments are *Carya ovata* 0.22 inch, *Quercus macrocarpa* 0.30 inch, *Q. velutina* 0.29 inch, *Acer saccharinum* 0.63 inch, and *Juglans nigra* 0.34 inch.—GEO. D. FULLER.

Inheritance of height in peas.—According to MENDEL'S original classic experiment with peas, the cross tall×dwarf gives a simple monohybrid ratio, with tallness dominant. The work of a number of recent investigators, however, has indicated that height in peas is a much more complex character, and that Mendel's 3:1 ratio by no means states the whole truth. WHITE[17] has made a critical examination of these investigations and has added some of his own. He concludes that there are at least 5 genetic factors involved, 2 for internode length, and 3 for number of nodes. He points out, however, that the same genetic pea material that MENDEL used will still give the 3:1 ratio. "The inheritance of height in peas has become complex only because of studies on new or distinctly different material, the characters of which, there is reason to believe, are due to distinct mutations."—MERLE C. COULTER.

Intercellular canals.—RECORD[18] has investigated the occurrence of intercellular canals in dicotyledonous woods, and has discovered 16 families in which they occur, mostly tropical. In some cases they are a normal feature of the wood, while in other cases they develop as a result of injury. They vary in direction and origin, in certain features resembling those of gymnosperms, but in many important features quite distinct. The secretions exhibit a wide range of variation, being resinous, oily, gummy, or tanniferous, as contrasted with conifers, in which the secretions are wholly resinous. RECORD concludes that the presence of intercellular canals in wood is a valuable diagnostic feature, and it was with this primarily in view that the investigation was made.—J. M. C.

Inheritance in Pisum.—WHITE[19] has presented a very significant paper on the interrelation of the genetic factors of *Pisum*. He has collected a mass of data of his own and also of earlier investigators of *Pisum*. He distinguishes 35 factors and discusses 5 linkage groups. A model section appears under the title "Modification of the expression of *Pisum* factors by different environments and by each other." This is one of the first successful attempts to make an intensive study of inheritance in plants, such as has been so well made on the fruit fly. Another such study, on corn, is now maturing at Cornell under the direction of Dr. R. A. EMERSON.—MERLE C. COULTER.

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[17] WHITE, ORLAND E., Inheritance studies in *Pisum*. III. The inheritance of height in peas. Mem. Torr. Bot. Club 17:316–322. *fig. 1*. 1918.

[18] RECORD, S. J., Intercellular canals in dicotyledonous woods. Jour. Forestry 22:429–441. 1918.

[19] WHITE, ORLAND E., Inheritance studies in *Pisum*. IV. Interrelation of the genetic factors of *Pisum*. Jour. Agric. Research 11:167–190. 1917.

Rusts of Oregon.—JACKSON[20] has published an annotated list of the rusts of Oregon, which brings together for the first time the rust flora of a state on the Pacific coast. All of the grain rusts recorded for North America (except *Puccinia Sorghi*) are known to occur in the state, and also all of the rusts of greenhouse crops. In addition to these, the Pacific coast rust of pears and quinces is said to be of considerable economic importance; and of course the forest-tree rusts represent an important field of investigation. The list includes 220 species of rusts occurring on about 500 different hosts, 8 of the species being described as new.—J. M. C.

Practical breeding.—COLLINS and KEMPTON[21] have given an excellent example of the effective application of the principles of pure science to the solution of a practical problem. The production of a race of sweet corn resistant to the earworm has been a strictly practical problem, and introduces no new phenomena or theories of inheritance. The authors, however, have established statistically the correlation between the amount of damage done by the earworm and certain superficial plant characters, and have followed this by selective breeding for those significant characters.—MERLE C. COULTER.

The morning glory in genetics.—BARKER[22] has found that the morning-glory is very favorable material for work in genetics. The almost innumerable combinations of floral colors are beautifully explained by the enzyme theory. "Each epistatic type is due to the addition of one or more genes, probably enzymatic in nature, which are not present in the hypostatic type."—MERLE C. COULTER.

Rusts of Cuba.—ARTHUR and JOHNSTON[23] have brought together all collections of Cuban rusts as a "basis for a thoroughly scientific and economic exploration of the island." The list includes 140 species, 12 of which are described as new, 15 are new to the North American flora, and 10 are exclusively Cuban.—J. M. C.

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[20] JACKSON, H. S., The Uredinales of Oregon. Mem. Brooklyn Bot. Gard. 1:198–297. 1918.

[21] COLLINS, G. N., and KEMPTON, J. H., Breeding sweet corn resistant to the corn earworm. Jour. Agric. Research 12:549–572. 1917.

[22] BARKER, E. E., Hereditary studies in the morning-glory (*Ipomaea purpurea*). Cornell Univ. Agric. Exper. Sta. Bull. no. 392. pp. 38. *pls.* 3. 1917.

[23] ARTHUR, J. C., and JOHNSTON, J. R., Uredinales of Cuba. Mem. Torr. Bot. Club 17:97–175. 1918.

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